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The Snakes of the Genus Storeria

Harold Trapido

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Introduction

The snakes of the genus *Storeria* are widespread in North America east of the Great Plains, ranging through Mexico to Honduras and in the northeast to southern Canada. In urban areas one species, *Storeria dekayi,* may thrive after most other snakes have long been exterminated. While considerable number of specimens have found their way into the collections of museums, no revision of *Storeria* has heretofore been attempted. The present paper presents the results of a comprehensive study of existing museum collections of this group of snakes. My principal emphasis has been on the study of variation within the species, the interpretation in taxonomic (and geographic) terms of such variation, and its bearing on the probable phylogeny within the genus. Several thousand specimens have been examined and the scale and coloration data tabulated. The scope of the work and the numbers of specimens entered in the tabulations have been limited by unforeseen circumstances; it is hoped that these studies together with obsrvation and experiment on the biology of some of the species may be resumed at a later date.

During the course of this study numerous individuals and institutions have been obliging in making loans of specimens and providing facilities for study. For such courtesies I am indebted to the following: E. Ross Allen, Silver Springs, Florida; Paul Anderson, Independence, Missouri; Dr. Reeve M. Bailey, Iowa State College; Roger Barbour, Morehead, Kentucky; Dr. Thomas Barbour, Arthur Loveridge and Benjamin Shreve, Museum of Comparative Zoology; Dr. S. C. Bishop, Arnold Grobman, and J. A. Tihen, University of Rochester; Br. Alexander Blouin, Mont-Saint-Louis College; Charles M. Bogert and Dr. James Oliver, American Museum of Natural History; Dr. G. D. Bunker and Dr. Clyde Hibbard, University of Kansas; Dr. Archie E. Carr and Coleman Goin, University of Florida; E. B. Chamberlain, Charleston

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I am particularly grateful to Mr. M. Graham Netting who kindly provided me with scale counts on West Virginia *Storeria* in the Carnegie Museum, to Dr. Hobart M. Smith, for assistance with the literature of the Mexican forms, and in other ways, to Dr. Edward H. Taylor who permitted me to examine his manuscript of the description of *Storeria hidalgoensis*, to Dr. Thomas Barbour who made special provisions to enable me to examine the critical collection at the Museum of Comparative Zoology, to Dr. and Mrs. A. H. Wright who have provided me with endless inspiration, and to Mr. Karl P. Schmidt for his generous expenditure of time in editing the manuscript, and his many helpful suggestions. For assistance in the preparation of photographs, I am indebted to Mr. Arthur L. Smith, and for help in preparing tables, checking data, typing, and in other ways, I am grateful to Mrs. Katharine Kapp.

Abbreviations of museum or private collection names which have been used in the text are as follows:

AMNH—American Museum of Natural History, New York, New York.
ANS—Academy of Natural Sciences of Philadelphia, Philadelphia, Pennsylvania.
CA—Chicago Academy of Sciences, Chicago, Illinois.
CAS—California Academy of Sciences, San Francisco, California.
CFK—Collection of Carl F. Kauffeld, Staten Island Zoo, New York, New York.
CHM—Charleston Museum, Charleston, South Carolina.
CLEM—Clemson College, Clemson College, South Carolina.
CM—Carnegie Museum, Pittsburgh, Pennsylvania.
CNM—Canadian National Museum, Ottawa, Ontario.
CORNELL—Cornell University, Ithaca, New York.
EHT-HMS—Collection of Edward H. Taylor and Hobart M. Smith, Lawrence, Kans.
ERA—Collection of E. Ross Allen, Silver Springs, Florida.
FMNH—Field Museum of Natural History, Chicago, Illinois.
FNB—Collection of Frank N. Blanchard (now in the Chicago Academy of Sciences, Chicago, Illinois).
INHS—Illinois State Natural History Survey Collection, Urbana, Illinois.
ISC—Iowa State College, Ames, Iowa.
JBH—Collection of J. B. Hollis, Henderson, Tennessee.
KU—University of Kansas Museum, Lawrence, Kansas.
LMK—Collection of Lawrence M. Klauber, San Diego, California.
MCZ—Museum of Comparative Zoology, Cambridge, Massachusetts.
OAM—Oklahoma Agricultural and Mechanical College, Stillwater, Oklahoma.
OUMZ—Ohio University Museum of Zoology, Athens, Ohio.
PA—Collection of Paul Anderson, Independence, Missouri.
RB—Collection of Roger Barbour, Morehead, Kentucky.
ROMZ—Royal Ontario Museum of Zoology, Toronto, Ontario.
S-M—Starr-Malnate collection of Edmund Malnate, Philadelphia Zoological Garden, Philadelphia, Pennsylvania.
SUMNH—Stanford University Museum of Natural History, Palo Alto, California.
UFC—University of Florida collection, Gainesville, Florida.
UMMZ—University of Michigan Museum of Zoology, Ann Arbor, Michigan.

UOMZ—University of Oklahoma Museum of Zoology, Norman, Oklahoma.
URMNH—University of Rochester Museum of Natural History, Rochester, New York.
USNM—United States National Museum, Washington, D.C.
ZSP—Zoological Society of Philadelphia, Philadelphia, Pennsylvania.

Complete synonymies for only the less well known forms are included, such as those from Mexico and Central America, and *S. d. obscura* from Florida.

In the tabulation of variation in head plates, the variations are given in per cent, and the symbols R and L refer respectively to right and left sides of the head. The tables showing variation in measurements and in numbers of body scales are greatly condensed. These data for the more abundant and wide ranging species may be analyzed in more detail in further studies on *Storeria*. The original data are available in a manuscript in the Cornell University Library submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy at Cornell University. In these tabulations the data for males and females are recorded separately with the exception of the figures for the sum of the ventrals and subcaudals in which the data for the two sexes are combined since there is no sexual variation.

A difficulty in the study of the snakes of the genus *Storeria* is that these, like many other snakes and lizards, become darkened and finally almost totally black upon preservation in formalin. The markings of the back and those about the head which show significant geographical variation are either partially or completely obscured in many specimens, so that it is not possible to designate their subspecies with certainty. Specimens of *Storeria* should be transferred to alcohol a short time after their fixation in formalin.

The working definition of species used here is that of a population having a distinctive combination of characters and exhibiting no overlap with related populations in these characters. This definition is used only since breeding experiments have not yet been made. It is understood that this is taken merely as an empirical measure of the more fundamental criterion, that of incompatibility in breeding. Subspecies are populations with distinctive combinations of characters occupying particular areas to the exclusion of other subspecies, but showing overlap in characters with other subspecies in the regions between the populations.

Storeria Baird and Girard

Storeria Baird and Girard, Cat. N. Amer. Rept., pt. 1, Serpents, p. 135, January 1853; Garman, N. Amer. Rept., pt. 1, Ophidia, p. 29, 1883; Cope, Rept. U. S. Nat. Mus., p. 1000, 1900.
Ischnognathus Duméril, Prodrome des Ophidiens, p. 468, May 1853; Duméril and Bibron, Erp. Gén., vol. 8, p. 506, 1854; Boulenger, Cat. Snakes Brit. Mus., vol. 1, p. 285, 1893.
Tropidoclonium Cope, Proc. Acad. Nat. Sci. Phila., p. 190, 1865, (partim).
Hemigenius Dugès, Proc. Amer. Philos. Soc., vol. 25, p. 182-3, 1888.
Natrix Cope, Proc. U. S. Nat. Mus., vol. 11, p. 391, 1889, (partim).

The "Catalogue of North American Reptiles" by Baird and Girard, in which the name *Storeria* is first used and defined, bears the date January 1853. The preface is dated January 5, 1853. Duméril's "Prodrome des Ophi-

diens," in which the name *Ischnognathus* is proposed for *Tropidonotus dekayi* appeared in the same year. Bocourt (1894: 742) indicates that Duméril's work was published in May; *Storeria* therefore has priority over *Ischnognathus*.

Garman in his "Reptiles of North America" (1883) modified the description of *Storeria* to include snakes with the loreal present or absent, and the anal entire or divided. He included the species *S. storerioides*, *S. occipito-maculata*, and *S. dekayi*, as well as *Microps lineatus* (=*Tropidoclonion lineatum*); this last with the anal plate entire.

Boulenger (1893) used *Ischnognathus* as the generic designation for this group and included *Regina kirtlandii* (*Natrix kirtlandii*) in addition to the forms treated under *Storeria* by Garman. The primary characters given for the genus were the number of maxillary teeth, 14 to 18, the equal maxillary and mandibular teeth, the keeled scales, the arrangement of the scales in 15 to 19 rows, and the presence of hypapophyses throughout the vertebral column.

Cope (1900) gave essentially the same diagnosis of the genus as Baird and Girard, mentioning in addition only the character of the teeth, "small, numerous, of equal length, and ungrooved." He referred to *Storeria* the species mentioned by Baird and Girard with the addition of his own *S. tropica*, described in 1885. *Storeria storerioides*, described in 1865 as *Tropidoclonium*, he here referred to *Natrix*, as this last genus has the loreal plate present.

There remains still the question as to how this group of snakes should be delimited. *Storeria dekayi*, *S. occipito-maculata*, *S. victa* and *S. storerioides* are very similar in appearance — size, proportions, scalation, and type of coloration. The presence of the loreal in *S. storerioides* sets it apart from the other forms, but in the large series of *S. dekayi* and *S. occipito-maculata* examined occasional specimens were found with the loreal present on one or both sides. The summation of the characters of *storerioides* indicates that this species is closest to the genus *Storeria*. *S. storerioides*, furthermore, does not fit elsewhere among related genera. It lacks the apical scale pits which are present in both genera to which Cope at different times assigned it — *Tropidoclonion* and *Natrix*. It further differs from *Tropidoclonion* in possessing a divided anal plate.

Taylor (1942) points out that *Adelophis copei* which Garman, Boulenger, and others included in the genus *Storeria*, properly has no place there. The chin shields are differently arranged, the prefrontals are enlarged to reach the upper labials, the anal plate is undivided, the upper labials are reduced to five, and the pattern is lineate.

We may characterize the genus *Storeria* as: colubrid serpents, with all teeth solid; teeth on the entire entire length of the maxillary and dentary bones; dentary bone hardly movable on the articular; hypapophyses present throughout the vertebral column; nostrils lateral; scales keeled, in fifteen to seventeen rows, without apical pits; head somewhat distinct from body; anal plate divided; subcaudals paired.

The scutellation of the head is of the normal colubrid type. The nostrils are within the limits of the nasal plates, which may be entire or divided to

form an anterior and a posterior nasal. The loreal may be present (regularly in *S. storerioides*, and as an anomaly in other species) or absent. The preoculars are normally one or two. The supraocular is single. The postoculars normally two or three in number. The anterior temporals are normally one, the posterior temporals generally two or three. The upper labials are normally six or seven; the lower labials normally seven. The chin shields are in two or three pairs, the anterior parallel and in contact medially, the posterior subparallel to divergent, in contact medially or separated by small scales.

This genus occurs in eastern North America from Quebec to Manitoba and south to Honduras.

KEY TO THE SNAKES OF THE GENUS STORERIA

A. Body scales in fifteen rows
- B. Loreal present .... *S. storerioides*, p. 5
- BB. Loreal absent
  - C. Supralabials seven, preoculars one .... *S. victa*, p. 39
  - CC. Supralabials six, preoculars two .... *S. occipito-maculata*
    - D. Venter whitish, head dark with a dark fork behind, fifth labial often obscured with black (Mexico) .... *S. o. hidalgoensis*, p. 14
    - DD. Venter red or pink (United States)
      - E. Three occipital light marks .... *S. o. occipito-maculata*, p. 20
      - EE. Occiput with light ring about two scales wide .... *S. o. obscura*, p. 33

AA. Body scales in seventeen rows .... *S. dekayi*
- F. Anterior temporal with a horizontal dark mark.
  - G. Chin shields in three pairs .... *S. d. anomala*, p. 73
  - GG. Chin shields in two pairs
    - H. Posterior temporals often three, sum of ventrals and subcaudals higher—av. 187 (Gulf Coastal Plain in Mexico) .... *S. d. temporolineata*, p. 70
    - HH. Posterior temporals two, sum of ventrals and subcaudals lower—av. 181 (Guatemala and Honduras) .... *S. d. tropica*, p. 77
- FF. Anterior temporal otherwise
  - I. Anterior temporal with a vertical or diagonal dark bar (occasionally interrupted); dorsal spots separate .... *S. d. dekayi*, p. 47
  - II. Anterior temporal with a vertical dark bar (occasionally interrupted); dorsal spots fused to short crossbars .... *S. d. wrightorum*, p. 57
  - III. Anterior temporal not marked with black, or with black only along margin; dorsal spots separate .... *S. d. texana*, p. 63

STORERIA STORERIOIDES (Cope)

Figs. 1-6

Tropidoclonium storerioides Cope, Proc. Acad. Nat. Sci. Phila., vol. 17, p. 190 and 197, 1865; Bull. U. S. Nat. Mus., vol. 1, p. 42, 1875; Yarrow, Bull. U. S. Nat. Mus., vol. 24, p. 18, 1883; Garman, Bull. Essex Inst., vol. 16, p. 24, 1884; Cope, Bull. U. S. Nat. Mus., vol. 32, p. 60 and 75, 1887; Proc. U. S. Nat. Mus., vol. 11, p. 392, 1888; Amaral, Mem. Inst. Butantan, vol. 4, p. 251, 1929.

Ischnognathus occipito-maculatus Fischer, Arch. Naturg., vol. 48, p. 284, 1882.

Hemigenius variabilis Dugès, Proc. Amer. Philos. Soc., vol. 25, p. 182-3, fig. 2, 1888; Dugès, La Naturaleza, (2), vol. 1, p. 403, pl. 27, fig. 14, 1890; Bocourt, Miss. Sci. Mex., vol. 13, p. 741-2, pl. 53, fig. 5, 1893; Cope, Amer. Nat., vol. 30, p. 1021 and 1025, 1896; Dugès, La Naturaleza, (2), vol. 2, p. 482-485, 1896; Taylor, Copeia, 1933, p. 97, 1933.

Natrix storerioides Cope, Proc. U. S. Nat. Mus., vol. 11, p. 392, 1889; Proc. U.S. Nat. Mus., vol. 14, p. 674, 1892; Amer. Nat., vol. 30, p. 1021 and 1025, 1896; Ann. Rep. U. S. Nat. Mus., p. 997-8, 1900; Dunn, Copeia, 1931, p. 163, 1931.

Ischnognathus storerioides Boulenger, Cat. Snakes Brit. Mus., ed. 2, vol. 1, p. 288-9, 1893; Günther, Biol. Cent. Amer., Rept., p. 136, 1894; Boettger, Nat. Rept. Senck. Mus., pt. 2, p. 31, 1898; Boulenger, Cat. Snakes Brit. Mus., ed. 2, vol. 3, p. 611, 1896; Werner, Zool. Jahrb., vol. 57, p. 38, 1929.

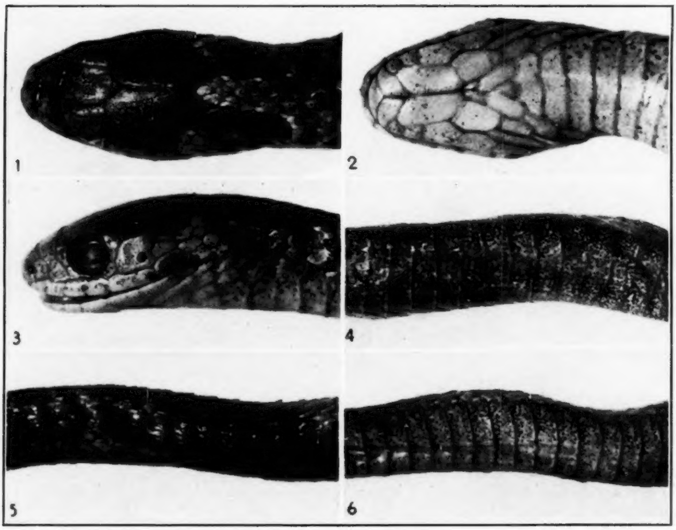
Tropidonotus storerioides Bocourt, Miss. Sci. Mex., vol. 13, p. 750, 1893.

Tropidonotus variabilis Günther, Biol. Cent. Amer., Rept., p. 133, 1894; Gadow, Proc. Zool. Soc. Lond., p. 231, 1905.

Thamnophis variabilis Amaral, Mem. Inst. Butantan, vol. 4, p. 147, 1929.

Storeria storerioides Garman, Mem. Mus. Comp. Zool., vol. 8, p. 29-30 and 143, 1883; Mertens, Abh. Ber. Mus. Magdeburg, vol. 6, p. 150, 1930; Taylor and Smith, Univ. Kans. Sci. Bull, vol. 25, p. 249-251, fig. 3, 1938; Taylor, Herpetologica, vol. 2, p. 79, 1942.

This is the one species of *Storeria* whose generic status has been questioned in recent times. Cope originally described the species in 1865 in the genus *Tropidoclonium* (=*Tropidoclonion*). Garman (1883) broadened the definition of *Storeria* to include this species (with a loreal). Dugès (1888) described the species *variabilis* for specimens from Guadalajara and Guanajuato, erecting the genus *Hemigenius* for it, since the specimens had the posterior chin shields somewhat reduced, so that he considered only one pair of chin shields to be present. Cope, in the following year, decided that his *storerioides* did not belong in the genus *Tropidoclonion* as originally described, since the anal



Figs. 1-6.—*Storeria storerioides.* All figures exceeding life size. Fig. 1. USNM 24989, Cotype, dorsal view of head and neck. Fig. 2. USNM 24989, Cotype, ventral view of head and neck. Fig. 3. USNM 24989, Cotype, lateral view of head and neck. Fig. 4. USNM 24987, Cotype, ventral view of body showing extent of dark punctulation. Fig. 5. USNM 24989, Cotype, dorsal view of body. Fig. 6. USNM 24989, Cotype, ventral view of body.

was not entire. He therefore placed it in *Natrix*, which has the anal divided. Boulenger (1893), and several European workers following him, included *storerioides* in their equivalent of *Storeria*, i.e. *Ischnognathus*. Bocourt (1893), not recognizing the identity of the *variabilis* of Dugès and the *storerioides* of Cope, included both in his treatment of the Mexican snakes, but placed *storerioides* in *Tropidonotus*. Günther (1894), like Bocourt, not only treated *variabilis* and *storerioides* as distinct species but placed them in different genera; *storerioides* in *Ischnognathus*, and *variabilis* in *Tropidonotus*. In 1929 Amaral added to this confusion by placing *variabilis* in *Thamnophis* despite the fact that the anal of that genus is entire, while in *variabilis* it is divided. He also listed *storerioides* in *Tropidoclonion*, which is also characterized by the entire anal. E. H. Taylor (1942) and H. M. Smith consider *storerioides* and *variabilis* to be congeneric and conspecific. In this I concur.

In the original description of this species the ventral and subcaudal scale counts, and the measurements of but one specimen are given, although as variations in the head plates are mentioned, it is evident that Cope had several specimens before him. No types were designated but the "habitat" of the species is given as the "Mexican plateau between the eastern ranges and the valley of Mexico." The specimens were sent to Cope by Dr. Charles Sartorius. In Cope (1900) the original description is merely transcribed with the exception that variation in the ventrals and subcaudals is noted, and the measurements, now in millimeters, not inches as before, are slightly different. Six specimens (USNM 9055-60) from Sartorius are listed. There are now four specimens in the U. S. National Museum designated as cotypes, and undoubtedly correctly so, although renumbered USNM 24987-90. In scalation these fall within the limits of variation given by Cope in 1900, but the extremes of ventral and subcaudal counts of the four specimens do not reach those given by Cope. These extremes are evidently those of the series of fifteen specimens cited by Boulenger (1893).

Hemigenius variabilis is apparently basd on a specimen from Barranca de Portillo, Guadalajara, and a second individual from Guanajuato. Taylor (1933) has located these types in the Alfredo Dugès Museo at the Colegio del Estado de Guanajuato.

DESCRIPTION

Diagnosis.—This is the only *Storeria* with a loreal normally present, and with the posterior chin shields normally separated from each other by small scales interposed between them. The occipital marks are also diagnostic, as they consist of a pair of elongate narrow dark marks, extending parallel to the body axis, behind the parietals. These are usually four or more scales in length. The dorsal scales are in lfteen rows with the lowermost normally smooth. The preoculars are normally two, postoculars two or three, the upper labials six or seven, the lower labials seven.

Scutellation.—Dorsal head scales normal; nostril opening at posterior margin of anterior nasal, anterior nasal separated from posterior nasal below nostril, and sometimes above; loreal present, variable in shape and extent,

sometimes entering the orbit between the preoculars; proculars normally two, the upper slightly larger; postoculars two or three, when two, the upper larger; anterior temporal single; posterior temporals normally two; upper labials normally seven, the third and fourth entering the orbit; lower labials normally seven, the fifth generally the largest; mental deltoid; chin shields in two pairs, the anterior pair slightly larger, or the two pairs subequal, the posterior pair separated by small scales; dorsal body scales in fifteen rows, keeled, except for the first row which has the scales smooth or very weakly keeled and twice as wide as those of the upper scale rows; second scale row more weakly keeled than rows above it and also slightly wider; scales emarginate behind, apical pits not apparent.

Ventrals in males 120 to 133 (nineteen specimens), in females 123 to 136 (twenty-one specimens); anal plate divided; subcaudals divided, in males 42 to 53 pairs (nineteen specimens), in females in 37 to 48 pairs (twenty-one specimens).

Coloration.—Head brownish with minute black punctulations aggregated to form dark areas of varying shapes, but always forming, toward the rear of the parietals, a pair of occipital marks extending from one to seven scales behind the parietals. These punctulations scattered along the side of the head, tending to be aggregated along the sutures of the labials and across the angle of the mouth. Dark markings weak or absent on the mental and chin shields. Body brownish above with a pattern of variously pronounced dorsal spots on the fifth and sixth scale rows; these spots fused to form crossbars on the body; alternating with the crossbars are faint lateral spots usually most pronounced on the fourth scale row. Body pattern, faint posteriorly, finally disappearing on the tail, formed by black margins of scales and black pigment on the skin between the scales. Lateral margins of ventrals and subcaudals with punctulations of varying intensity; their extent is quite variable, some specimens being so faintly marked that the belly appears clear, while others have an intensification of these fine spots so that the belly appears black laterally, with a narrow midventral light stripe only a millimeter wide.

Hemipenis.—The retractor penis muscle inserts at the level of nineteenth subcaudal scale. The penis itself apparently extends as far as the eighth subcaudal. There are small fine spines distally; the spines become larger proximally, the longest being about two millimeters from the base of the organ, which bears smooth spineless folds. The spines of the basal half of the organ are larger than in other species of *Storeria,* but there is no single much enlarged spine as in *S. dekayi.* The distal half of the organ has its dorsal surface thrown into a large fold so that when everted it is probably expanded as in *S. occipito-maculata.* The sulcus spermaticus could not be made out in the dissected hemipenis.

The hemipenis is more similar to that of *S. occipito-maculata* than to that of *S. dekayi.* The hemipenis of *S. storerioides* differs from that of *S. occipito-maculata* in its relatively larger proximal spines.

Dentition.—The maxillary teeth are thirteen to fifteen, the last of the

series enlarged; the dentary is provided with approximately eleven teeth, subequal in length, but with a trend toward a reduction in size posteriorly.

Size.—The largest male examined is 328 mm. long (EHT-HMS 21423 from Rio Frio, Mexico) and the largest female is one recorded by Boulenger (1893), 340 mm. in total length. The ratio of tail to total length in males is 21 to 25 per cent (average 22 per cent) in females 19 to 21 per cent (average 20 per cent).

DESCRIPTION OF COTYPES

The scutellaticn of the four cotypes in the United States National Museum may be summarized as follows:

No.	Sex	Ventrals	Subcaudals	Supralabials	Infralabials	Postoculars	Posterior temporals	Total Length	Tail Length
24987	♀	123	43	6/6	7/7	3/2	3/2	320	63
24988	♂	126	47	7/7	7/7	2/3	3/2	309	69
24989	♂	125	49	7/6	7/7	3/3	2/3	271	61
24990	♂	127	47	6/6	7/6	3/3	3/2	260	56

The preoculars are invariably 2/2, the anterior temporals 1/1, the dorsal scales in 15 rows, and the posterior chin shields separated. The loreal is invariably present, entering the orbit between the preoculars in No. 24987, excluded from the orbit in the remaining three.

Coloration in cotypes.—USNM 24988 is a brown specimen like *S. dekayi,* while the other three are grayer, 24987 being decidedly dark gray. The dorsal markings are prominent, except in 24988.

The top of the head is brownish or tan peppered with black. The sides of the head are less heavily peppered, but with specific areas of intense pigmentation. The dark color of the top of the head ends about the middle of the upper postocular, and extends along the upper margin of the anterior temporal. The occipital marks are darker than the head. The markings of the upper labials are variable, but in general there is a small dark spot below the eye, on the third labial (in six labial specimens) or fourth labial (in seven labial specimens). This condition is most pronounced in 24988, in which there is also a dark spot on the rear of the fourth upper labial. The ventral half or three-fourths of the last labial is dark and the mark extends forward to involve the rear lower corner of the penultimate labial. The lower labials, mental, and chin shields are almost unspotted or very weakly flecked. The dorsal crossbars extend down to the fifth scale row and vary in width from a fourth to a whole scale.

There are fifty-two to sixty-two cross bands on the body. No. 24988 has five pairs of spots on the neck not fused to form crossbars. There are smaller, faint marks on the third scale row.

The black flecks which darken the back become more scattered on the venter but in 24987 the belly is blackish except for a narrow central area one-third of the width of the ventrals. Nos. 24989 and 24990 have less pigmentation of the belly while 24988 has the belly about as unmarked as most *S. dekayi,* i.e., with only a few scattered flecks along the side of the ventrals.

VARIATION

Scutellation.—Variation in numbers of ventrals and subcaudals is shown in Table 1. The portions of the table summarizing the data on the ventrals and the subcaudals include all the specimens seen by the writer, and the counts given by Boulenger (1893: 288-9, 1896: 611) on the series of specimens in the British Museum. In the part of the table dealing with the ventrals minus the subcaudals the counts of Boulenger (1893: 288-9) are omitted since he lists ventral and subcaudal counts separately and the two may not be related with certainty.

There is a slightly higher number of ventrals and a somewhat more decidedly lower number of subcaudals in females.

It is difficult to correlate trends in scale variation with the geographic or ecological factors, since the material now available often has vague locality data, and since variation in altitude is great over relatively short distances in the terrain occupied by this species in central Mexico. Altitudinal data, much less ecological data, are woefully lacking in other than recently collected material. There is, however, some indication that specimens from lower altitudes at the periphery of the range of this species tend to have lower numbers of ventrals.

The specimens with the low subcaudal counts (i.e., 42 to 46 in the males and 37 and 38 in the females) are from the northern and northwestern periphery of the range of the species, and from low altitudes (4500′-6000′). Thus the female with 37 subcaudals is from Autlan, Jalisco, those with 38 are from Talpa and Mascota in Jalisco and from Jesus Maria in San Luis Potosi. The male with 42 subcaudals is from Talpa, Jalisco, the ones with 45 are from

TABLE 1.—Variation in Certain Characters of *Storeria storerioides.*

Ventrals

No. of scales	120	'1	'2	'3	'4	'5	'6	'7	'8	'9	130	'1	'2	'3	'4	'5	'6
♂	1	1				2	2	3	1	2	3	4		2			
♀				1			1	1	1	2	5	4	2	1	2		2
total	1	1	0	1	0	2	3	4	2	4	8	8	2	3	2	0	2

Subcaudals

Scales	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53
♂						1			2	1	4	2	2	3	3	2	1
♀	1	4		5	5		1	1	2	1	1	1					
total	1	4	0	5	5	1	1	1	4	2	5	3	2	3	3	2	1

Ventrals — Subcaudals

No. of scales	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90	91	92
♂	1	1	1	2	3	4	2	1										
♀						1		2			2	1		1	1	2	3	1
total	1	1	1	2	3	5	2	3	0	0	2	1	0	1	1	2	3	1

Talpa, and north of the Rio de Santiago, Jalisco, and the one with 46 subcaudals is from Autlan, Jalisco. Thus there is some evidence of reduced subcaudal numbers in specimens from Jalisco and San Luis Potosi but any subspecific distinction must await the collection of more ample data.

The variations in head plates in the twenty-six specimens examined are summarized in Table 2. The labials are exceedingly variable, with the fusion in the supralabials either before or to the rear of the orbit. The reduced number of infralabials is mostly due to the fusion of what are normally the second and third, although the last two may be fused. When there is reduction in the labials on both sides, the fusions are bilaterally symmetrical, i.e., the variations on each side involve the same scales. When the loreal enters the eye it is not quadrilateral, but elongate and acute posteriorly, wedged between the two preoculars.

In the variability of its head plates *storerioides* must be considered the most plastic of the species of *Storeria.*

Coloration.—The dark occipital marks are usually diagnostic of this species, being longer than broad in contrast to *S. dekayi* in which they are

TABLE 2.—Summary of Variation in Head Plates in 26 Specimens of *Storeria storerioides* Cope.

Supralabials	5–R	6–R	6–L	6/6	7/7			
Frequency in Per Cent	3.8	3.8	7.6	26.6	normal			
Infralabials	5–L	6–R	6–L	6/6	7/7	8–R		
Frequency in Per Cent	3.8	7.6	7.6	7.6	normal	3.8		
Preoculars				1–R	2/2	3–L		
Frequency in Per Cent				3.8	normal	3.8		
Postoculars					2/2	3–R	3–L	3/3
Frequency in Per Cent					normal	3.8	7.6	15.2
Posterior Temporals				1–L	2/2	3–R	3–L	3/3
Frequency in Per Cent				3.8	normal	26.6	11.4	7.6
Loreal Enters Orbit		Rt. Side		Left Side		Both Sides		
Frequency in Per Cent		3.8		3.8		7.6		

broader than long or reduced to small spots. These occipital marks are variable in length, but one specimen (EHT-HMS 5404 from Zitacuaro, Michoacan) has no occipital marks other than the anteriormost of the paired body spots. The occipital paired marks may be equal or of different lengths. Thus one specimen has the occipital marks extending five scales posterior of the parietals on one side, seven on the other. Most frequently these marks extend four scales behind the parietals.

Taylor and Smith (1938) record an irregular narrow reddish-brown band on the middorsal line and Boulenger (1893) says the species is gray or reddish beneath. Dugès (1888) states that, "La couleur général varie du brun jaunâtre au rouge brique sur les parties superieures. . . ." He also notes that the throat is white, and the venter brick red to yellowish white. These colors are lost in preserved material.

A specimen from Guadalajara, Jalisco, USNM 29125, is melanistic. The head coloration is normal, but with an intensification of the punctulations. The chin and first several ventrals are likewise normal, but the dorsum of the body and tail have the pattern obscured with black, while ventrally the punctulations are concentrated and similarly appear black, with a faint light midventral area for the first third of the body. Some of the body scales, on

close examination, are white margined, as is some of the skin between the scales, so that the normal pattern may be made out vaguely when the specimen is submerged in liquid.

Other specimens from Guerrero are also very dark, but possibly as a result of poor preservation. There may be a distinct geographic race in lower altitudes in Guerrero but the material now available is not sufficient to define it.

DISTRIBUTION

This species is known only from the southern part of the Mexican plateau and the adjoining Sierra Madre Occidentale and Sierra Madre del Sur, where it occurs at altitudes of 4500 to 10,500 feet. It ranges from Morelos north to southern San Luis Potosi on the Plateau, and north to central and western Jalisco in the west. An isolated record from far to the northwest at "Ciudad in Durango" (Günther, 1894) is open to question until further specimens are found. Specimens from the region of the Sierra Madre del Sur are probably separated from direct contact with the central population by the low valley of the Rio Balsas. There is the possibility that the range of these snakes is connected through the highlands of northwestern Oaxaca and Puebla, around the Balsas basin, but specimens to confirm this are lacking.

In terms of the biotic provinces of Mexico as recently outlined by Smith (1939, 1940), *Storeria storerioides* is confined to the southern nearctic provinces; the Guerreran, Austro-central, and Austro-oriental.

AFFINITIES

Storeria storerioides seems in all regards to be closest to the stock from which the genus *Storeria* arose. Of the existing species in the genus it is most closely related to *Storeria occipito-maculata* through its southern race, *hidalgoensis*. It agrees with *occipito-maculata* in having fifteen scale rows and two preoculars as well as certain salient features of coloration such as the stippling of the lateral edges of the ventrals. While the upper labials are normally seven in *S. storerioides,* they are reduced to six on each side, the normal number for *S. occipito-maculata,* in no less than twenty-seven per cent of the specimens examined. The high percentage of variability in the head plates of this species suggests a plasticity that includes the genetic potentialities found in the other members of the genus.

The limitation of this species to the relatively humid and temperate uplands in the southern part of the Mexican plateau, and its faunal relations along the Sierra Madre Orientale are easily understood. To the northwest the arid northern Mexican plateau forms a barrier for snakes with the mesic environmental requirements of this genus (especially as to cover and food). To the west and south the limits of the species are established by the rapid drop in altitude to tropical conditions. The competition of the large number of neotropical species reaching the northern limits of their range in the region of the Isthmus of Tehuantepec forms a part of the southern ecological barrier.

Storeria occipito-maculata is principally an upland species like *S. storerioides,* and as the southern limits of its range (in the subspecies *hidalgoensis*)

coincide with the northern periphery of the range of *S. storerioides,* it is the logical derivative of that form. *Storeria occipito-maculata,* like *S. storerioides,* is conspicuously absent in the lowlands of the eastern Mexican coastal plain. *Storeria dekayi* is also thought to be derived from the *S. storerioides* line (see below, page 80).

LOCALITY RECORDS

Specimens examined as follows:

DISTRITO FEDERAL: Desierto de los Leones, 10,000 feet, EHT-HMS 5354-5.

GUERRERO: Omilteme, Sierra de Burro Mountains, MCZ 42663; Chilpancingo, FMNH 38346-7.

JALISCO: Guadalajara, USNM 29125.

MEXICO: Llano Grande, five miles west of Rio Frio, USNM 110325-6; Nevada de Volcán Toluca, EHT-HMS 16141; Rio Frio, 9,500 feet, EHT-HMS 5403, 21422-23; Km. 57 on road to Puebla, near Rio Frio, 9,500 feet, EHT-HMS 5352; Km. 66 on road to Puebla, near Rio Frio, 9,500 feet, EHT-HMS 5353; Ten miles west of Villa Victoria, USNM 110327.

MICHOACAN: Two miles south of San Martin near Zitacuaro, EHT-HMS 5404.

MORELOS: Lake Zempoala near Tres Cumbres, 10,500 feet, EHT-HMS 5351, 5594-5; Tres Cumbres (Tres Marias), EHT-HMS 4665.

SAN LUIS POTOSI: Mountains near Jesus Maria, USNM 46428.

NOT ASSIGNABLE TO STATES: "Mexico," MCZ 25879; "Mexican Plateau between eastern range and valley of Mexico," USNM 24987-90, COTYPES; "Uncertain Locality, perhaps Zempoala," Morelos, EHT-HMS 5356.

Also recorded as follows: (general localities like "Mexico" omitted).

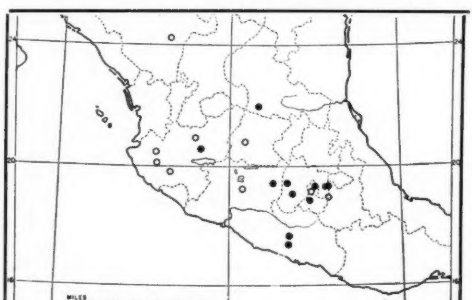
DISTRITO FEDERAL: Mexico City (Günther, 1894).

DURANGO: "Ciudad in Durango" (Günther, 1894).

GUERRERO: Amula (Boulenger, 1896).

GUANAJUATO: Guanajuato (Dugès, 1888; Dugès 1890; Bocourt, 1893; Günther 1894; Dugès 1896; Amaral, 1929).

JALISCO: Autlan, Colonia Brizuela, Hacienda el Rosario (Boulenger, 1893); Guadalajara, Barranca de Portillo (Dugès, 1888; Dugès, 1890); Guadalajara (Günther, 1894); Mascota, Hacienda Sta Gertrudio (Boulenger, 1893); North of Rio de



Map 1. Distribution of *Storeria storerioides.* Black spots represent specimens examined, circles records from the literature. (Based on Field Museum Outline Map No. 1.)

Santiago (Boulenger, 1895); Talpa, La Cumbre de los Arrastrados (Boulenger, 1893); "Jalisco" (Dugès, 1896); "Jalisco," 8500 feet (Boettger, 1898).

MEXICO: "Mexico State" (Mertens, 1930).

MICHOACAN: Morelia (Dugès, 1896).

NOT ASSIGNABLE TO STATES: "en el Valle de Mexico" (Dugès, 1890); Plateau of Mexico (Boulenger, 1893); Popocatepetl, 9000 feet (Boulenger, 1896); the high plateau, 6000-8000 feet (Gadow, 1905).

STORERIA OCCIPITO-MACULATA HIDALGOENSIS Taylor

Mexican Red-bellied Snake

Figs. 7-10

Ischnognathus occipitomaculata Müller, Reisen Ver. Staat. Can. Mex., p. 611 *fide* H. M. Smith *in litt.*, 1865; Dugès, La Naturaleza, vol. 1, p. 144, 1870.

Storeria occipitomaculata Cope, Proc. Amer. Philos. Soc., vol. 22, p. 386, 1885; Bull. U. S. Nat. Mus., vol. 32, p. 75, 1887; Proc. U. S. Nat. Mus., vol. 14, (882), p. 675 (partim), 1891; Amer. Nat., vol. 30, p. 1023 (partim), 1896; Ann. Rept. Smithsonian Inst., p. 1003-5 (partim), 1900; Stejneger and Barbour, Check List N. Amer. Amph. Rept., ed. 4, p. 131 (partim), 1939.

Storeria occipito-maculata Bocourt, Miss. Sci. Mex., vol. 13, p. 745-6, pl. 53, fig. 6 (partim), 1893; Stejneger and Barbour, Check List N. Amer. Amph. Rept., ed. 1, p. 98 (partim); Dunn, Proc. Acad. Nat. Sci. Philad., vol. 88, p. 477, 1936.

Ischnognathus occipito-maculatus Günther, Biol. Cent. Amer., Rept., p. 136 (partim), 1894.

Storeria sp., Taylor, Univ. Kans. Sci. Bull, vol. 27, p. 113, 1941.

Storeria hidalgoensis Taylor, Herpetologica, vol. 2, p. 78, 1942.

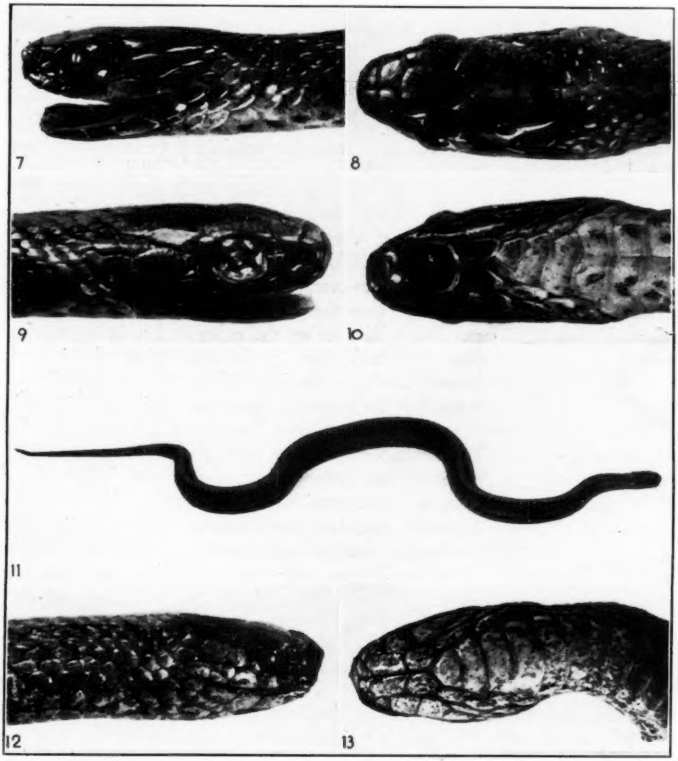
This race from the Sierra Madre Orientale of northeastern Mexico has not been distinguished from *Storeria occipito-maculata* until recently, although Dunn (1936) recognized that it might represent a new "color race." Taylor (1942) regards it as a full species, but from examination of the series of three dozen specimens available to me it is now apparent that it should be regarded as a race of *S. occipito-maculata*. The holotype is in the Edward H. Taylor-Hobart M. Smith collection at Lawrence, Kansas.

DESCRIPTION

Diagnosis.—Characters mostly as for *Storeria o. occipito-maculata*, differing as follows: head darkened, and with a black wedge-shaped mark extending behind each parietal; fifth labial often obscured with black; belly usually white or gray, size large, ventrals high (males 124 to 134, females 128 to 136); posterior nasal enlarged.

Scutellation.—The head plates are in general similar to those of *S. o. occipito-maculata*. Dorsal head plates normal; nostril opening with posterior border along suture between nasals; posterior nasal two or more times the area of the anterior nasal; loreal absent; two preoculars subequal in area; postoculars two, the upper larger; temporals normally 1-2, the anterior usually larger than the combined area of the posterior; upper labials normally six, the third and fourth entering the orbit, the fifth largest, the sixth somewhat smaller and those anterior smallest; lower labials normally seven, the fourth and fifth

largest, the first pair in contact between the mental and the anterior chin shields; mental triangular, broader than long; chin shields in two pairs, the anterior in contact throughout their length, a little less than twice as long as broad, laterally in contact with the first to fourth infralabials; posterior chin shields slightly shorter than anterior, truncate anteriorly and rounded posteriorly, in contact for three-fourths or more of their length, laterally in contact with the fourth and fifth infralabials; dorsal body scales in 15 rows, all keeled, the first row about twice as broad as the others and very weakly keeled, scales



Figs. 7-10. *Storeria occipito-maculata hidalgoensis*. Views of head and neck of specimen from Alvarez, San Luis Potosi, in the collection of the Museum of Comparative Zoology (several times life size). Fig. 11. *S. o. occipito-maculata*, photographed in life from a specimen from Ithaca, New York, less than life size. Fig. 12. *S. o. occipito-maculata*, lateral view of head several times enlarged, specimen from Ithaca, New York. Fig. 13. *S. o. occipito-maculata*, ventral view of head several times enlarged, specimen from Ithaca, New York.

truncate or weakly emarginate posteriorly, scales of first row not emarginate, apical pits not apparent.

Ventrals in males 124 to 134 (fourteen specimens), in females 128 to 136 (twenty-three specimens); anal plate divided; subcaudals divided, in males 52 to 63 (fourteen specimens); in females 47 to 53 (twenty specimens).

Coloration.—The general features of the color pattern of *Storeria occipito-maculata* are described in the account of the typical subspecies.

The dorsal color on the body in *S. o. hidalgoensis* varies from light brown or tan to reddish or grayish. The ground color is usually brown flecked with variable amounts of gray so that the snakes are "brownish" or "grayish," depending on the amount of flecking, just as in subspecies *occipito-maculata*. The dark flecking on the first and sixth scale rows is usually faint or absent, but such flecks, as well as some white, may be present. In some specimens from Alvarez the marks on the sixth scale row are joined to form small spots somewhat in the fashion of the marks on the dorsum of *S. dekayi*.

In specimens from Hidalgo the dorsal coloration extends as faint and diffuse markings on the edges of the ventrals, but certain of those from Alvarez, San Luis Potosi, have three-fifths of the ventrals obscured with black. Others from the same locality, however, have the belly almost clear and unmarked. Unfortunately, any red on the ventrals fades with time on preservation, so that it is impossible to determine the color in life in most of the material of this race. According to Taylor, in the description of this snake, the type had the belly ivory-white with no trace of red. Dunn (1936), who had recently collected material at his disposal, found the bellies gray in all but one of five specimens from Pablillo, Nuevo Leon, and Alvarez, San Luis Potosi. As the pink-bellied Pablillo specimen is from the north and may represent an approach to subspecies *occipito-maculata,* the normal belly color in life for *hidalgoensis* may be white or grayish. W. W. Brown, the collector of the large series from Alvarez deposited in the Museum of Comparative Zoology, informs me that to the best of his memory these snakes were reddish below in life; but this is a recollection after more than fourteen years, and accordingly open to question.

In this race, as in the subspecies *obscura,* there is a constant pronounced blackening of the head, particularly toward the rear. The black is prolonged behind the parietals, forming a pair of wedge-shaped marks two scales in length. These markings are interposed between the light occipital marks, when the latter are present. The occipital light marks may be present, or the neck may be about the same color as the dorsum. The condition of the side of the head and the lower jaw is variable. In some specimens from Alvarez, black obscures the labials, mental, and chin shields completely, while others, from Alvarez and elsewhere have the fifth labial lighter or even white, and the mental also unmarked. According to Taylor (1942) the fifth supralabial is lighter than the others in the type. The fifth supralabial may be black on one side and light on the other in individual specimens. Those with the fifth

supralabial light have the rear and labial margin of the scale dark as in subspecies *occipito-maculata* and unlike *obscura*. Specimens which have been preserved a long time, (such as ANS 11680 and 14754-5) have the dark pigment of the labials faded. The lower jaw may be light and only stippled with black.

Size.—The largest male examined was 337 mm. in total length (eleven specimens), the largest female 333 mm. (twenty-two specimens). A summary of the average total length and tail/total length ratio is given in Table 3. If the average total length of subspecies *hidalgoensis* as determined in the sample now available is a true representation of the natural population it will be seen that the snakes of this race are considerably larger than those of the other subspecies. The tail/total length ratio does not differ from subspecies *occipito-maculata*.

VARIATION

Scutellation.—The variation in ventrals and subcaudals is summarized in Table 3. It will be seen that while there is a slight difference in the average number of ventrals in males and females (the females having the greater number), there is great overlap in the extremes. The number of ventrals is greatest to the south (in Hidalgo) and lower in the north (in Nuevo León). The number of ventrals in subspecies *hidalgoensis* exceeds that of most *S. o. occipito-maculata*. This species is uncommon at the western edge of its range, so that an adequate sample from the westernmost area occupied by *occipito-maculata* in the United States is not available to determine if there is a gradual transition from the one race to the other.

The sexual difference in number of subcaudals is somewhat more pronounced than is the difference in number of ventrals. The number of subcaudals is higher in the males. As with the ventrals, the number is higher to the south and lower to the north. It will be pointed out that in *S. o. occipito-maculata* there is an increase in number of subcaudal scales from the northeast southward to the lower Mississippi Valley. The subcaudals in the Mexican *hidalgoensis* show the continuation of this clinal trend.

The cline within subspecies *hidalgoensis* is best shown by the figures for ventrals plus subcaudals, disregarding sex:

	Number	Extremes	Average
Nuevo Léon	3	176-179	177.3
San Luis Potosi	25	178-190	183.2
Hidalgo	4	186-195	191.0

The variation in head plates in this race is relatively slight. There are two preoculars, two postoculars and two anterior temporals in all specimens examined. The supralabials may be reduced to five or increased to seven (see Table 4). The infralabials are less variable, the only abnormality observed being the increase to eight on one side. The posterior temporals are occasionally one or three instead of the normal two. The posterior nasal which is variable in size in subspecies *occipito-maculata* here seems to be consistently about twice the

TABLE 3.—Summary of Regional Variation in Certain Characters of *Storeria occipito-maculata hidalgoensis.*

	Males			Females		
	No.	Extremes	Average	No.	Extremes	Average
Ventrals						
Nuevo Léon	2	124-125	124.5	1	128-128	128.0
S. L. P.	9	125-134	129.2	19	130-136	132.7
Hidalgo	3	130-133	131.3	3	131-135	132.7
Subcaudals						
Nuevo Léon	2	52-52	52.0	1	51-51	51.0
S. L. P.	7	54-62	56.9	18	47-53	49.8
Hidalgo	3	59-63	61.3	1	51-51	51.0
Ventrals—Subcaudals						
Nuevo Léon	2	72-73	72.5	1	77-77	77.0
S. L. P.	7	66-76	71.4	18	79-86	82.9
Hidalgo	3	68-71	70.0	1	84-84	84.0
Total Length						
Nuevo Léon	2	218	217	1	240	240
S. L. P.	7	313	275	18	333	303
Hidalgo	2	337	310	3	332	301
Tail/Total Length Ratio						
Nuevo Léon	2	24.3-25.1	24.7	1	22.5-22.5	22.5
S. L. P.	7	24.0-27.2	25.2	18	20.1-24.0	21.8
Hidalgo	3	23.5-26.0	24.9	1	20.8-20.8	20.8

area of the anterior nasal. This condition is sometimes matched in subspecies *occipito-maculata* but it is nowhere as constant as in the series of *S. o. hidalgoensis.*

HABITAT

According to Taylor (1941) and Cope (1885) the characteristic plants of the region inhabited by this snake in Hidalgo are pines, firs, and alders, as well as brake fern and shrubs of the genera *Andromeda* and *Vaccinium.* At the high altitudes in which this race occurs the climate is humid and many damp situations are available.

DISTRIBUTION

Storeria occipito-maculata hidalgoensis is known from high altitudes in the Sierra Madre Orientale from Hidalgo north through eastern San Luis Potosi to Pablillo, Nuevo León. The altitude range is from about 6000 feet to about 8000 feet. In a list of the vertebrate animals of Mexico, Dugès (1870) has also recorded its from Guanajuato and Guadalajara, but these records are doubtful. Cope (1900) gives the range of this snake as south to Vera Cruz, and he has been followed in this by Stejneger and Barbour (Check List, ed. 1, 1917, and subsequent editions), but there do not appear to be any authentic records from that state.

AFFINITIES

This snake is obviously most closely related to *Storeria o. occipito-maculata.* The scalation is the same except that the ventrals are higher in number, and the subcaudals somewhat so. The distinctive coloration is a modification of the fundamental color pattern of *S. o. occipito-maculata,* or perhaps

TABLE 4.—Summary of Variation in Head Plates in 35 Specimens of *Storeria occipito-maculata hidalgoensis*.

Supralabials	5–R	5–L	6/6	7–R	7–L
Frequency in per cent	2.9	5.7	normal	2.9	2.9
Infralabials			7/7	8–L	
Frequency in per cent			normal	5.9	
Posterior Temporals	1/1		2/2	3–R	3/3
Frequency in per cent	2.9		normal	8.6	2.9

more correctly, the pattern in subspecies *occipito-maculata* is modified from *hidalgoensis*. To the north, the high mountains which provide the humid habitat for this race, give way to the semiarid southern Great Plains where these mesic snakes find no congenial habitat. In consequence, *S. occipito-maculata* barely reaches Texas and Oklahoma, and this area is, in effect, a barrier separating the population of subspecies *hidalgoensis* in the northeastern Mexican mountains from that of *occipito-maculata* in the moist Ozark Plateau and the Mississippi valley. While there are reservoirs of suitable habitats for this species in the river valleys of Texas, the drainage from northwest to southeast lies athwart the path of migration which the species would have to follow. A further discussion of the relations of these two subspecies will be found in the account of *S. o. occipito-maculata*.

To the south and west of the area occupied by *S. o. hidalgoensis*, *S. storerioides* occurs in similar high country. The scale rows in these two are the same, fifteen. *Storeria storerioides* is distinctive in the possession of a loreal, but the enlarged posterior nasal of *hidalgoensis* suggests that the loreal of *storerioides* has been lost in evolution by a fusion with the posterior nasal resulting in the large plate found in *hidalgoensis*. There are frequently six supralabials in *storerioides*, the normal number in *hidalgoensis*. The dark wedge marks to the rear of the parietals in *hidalgoensis* resemble the pair of elongate dark markings behind the parietals in *storerioides*. It is significant that the belly in *hidalgoensis* is white or gray, just as in *storerioides*. The only definitely red-bellied specimen of *hidalgoensis* is from the northern edge of the range of this race in Nuevo León, where I believe the red-bellied race, *occipito-maculata*, to have influenced the southern form. While the hemipenis in *S. o. hidalgoensis* has not been available for dissection, it is to be presumed that it is similar to that of *S. o. occipito-maculata* and to that of *S. storerioides*. On the basis of these various data it seems evident that *S. o. hidalgoensis* is derived from *S. storerioides*, though now more closely related to *S. o. occipito-maculata*.

LOCALITY RECORDS

Specimens examined as follows:

HIDALGO: Zacualtipán, ANS 11680, 14754-5; near Zacualtipán, EHT-HMS 23624; near Durango, EHT-HMS 23625.

NUEVO LEON: Hills above Pablillo, ANS 20025-7.

SAN LUIS POTOSI: Vicinity of Alvarez, alt. 8000 feet, MCZ 19016-8, 19020, 25006-19, 25020 (eight specimens), ANS 20098, 20100.

STORERIA OCCIPITO-MACULATA OCCIPITO-MACULATA (Storer)

Red-bellied Snake

Figs. 11-13, 20

Coluber occipito-maculatus Storer, Rept. of Mass., p. 230, 1839; Boston Journ. Nat. Hist., vol. 3, (1-2), p. 33-34, 1840.

Coluber venustus Hallowell, Proc. Acad. Nat. Sci. Phila., vol. 3, p. 278-280, pl. 3, 1848.

Storeria occipito-maculata Baird and Girard, Cat. N. Amer. Rept., pt. 1, Serpents, p. 137, 1853.

Ischnognathus occipitomaculatus Günther, Cat. Snakes Brit. Mus., p. 81, 1858.

Storeria occipitomaculata Stejneger and Barbour, Check List N. Amer. Amph. Rept., ed. 4, p. 131, 1939.

Storeria occipito-maculata was described from a preserved specimen, and the most obvious character in life, the red belly, was not apparent. The type, from Amherst, Massachusetts, had six upper labials, seven lower labials, one

Map 2. Distribution of *Storeria occipito-maculata*. The black spots represent isolated records, presumably outside the general range of the species. (Based on Goode Base Map No. 109. By permission of the University of Chicago Press.)

hundred and twenty-four ventrals and thirty-eight subcaudals. It was ten and one-half inches in total length. The upper part of the body was gray, with a faintly lighter stripe down the back which was bordered on each side with a row of dark colored scales; the belly was yellowish white, with black markings on the edges of the plates, which anteriorly appeared like black dots; there were "three large white irregularly formed blotches directly back of the occipital plates; one above, and one on each side of the first."

Hallowell's *Coluber venustus* is based on a specimen of *S. occipito-maculata* from Copper Harbor, Lake Superior, Michigan, in the collection of the Academy of Natural Sciences of Philadelphia (ANS 5907). It is still in good condition.

The type of *S. o. occipito-maculata* is presumably no longer in existence.

DESCRIPTION

Diagnosis.—The subspecies *occipito-maculata* is characterized by the three light spots on the occiput, the light mark on the fifth labial scale interrupted by black on the lower margin of the scale, the moderate amount of black pigment over much of the dorsum and rear of the head, and the red belly. The dorsal scales are keeled, and in fifteen rows. The loreal is absent, the preoculars normally two, the postoculars normally two, the upper labials normally six, and the lower labials seven.

Scutellation.—Dorsal head scales normal; anterior nasal slightly smaller than posterior nasal, or subequal, approximately equilateral, frequently fused with the latter; posterior nasal approximately equilateral; loreal normally absent; two preoculars usually about equal; supraocular about twice as long as wide; two postoculars, the upper usually slightly larger; temporals normally 1-2, the anterior usually slightly larger than the posterior temporals combined; upper labials normally six, the third and fourth entering the orbit, the fifth and sixth about equal, and larger than the others; lower labials normally seven, the fourth and fifth largest, first pair in contact between the mental and anterior chin shields; mental triangular, broader than long; chin shields in two pairs, the anterior twice as long as broad, normally in contact throughout their length along the median line, in contact with the first to the fourth infralabials laterally; posterior chin shields normally shorter than anterior, truncate anteriorly and gently tapering to a rounded apex posteriorly, normally in contact for the anterior third of their length, but divergent and separated posteriorly by small scales, laterally in contact with the fourth and fifth infralabials; dorsal body scales in fifteen rows (sometimes seventeen to twenty-two rows on the occiput), all keeled except a few on the occiput, first scale row broader than others, scales becoming gradually narrower dorsally, scales emarginate behind, apical pits not apparent.

Ventrals in males 110 to 132 (three hundred and forty-six specimens), in females 115 to 133 (three hundred and eighty-four specimens); anal plate divided; subcaudals divided, in males 42 to 61 (three hundred and thirty-

seven specimens), in females 35 to 54 (three hundred and sixty-three specimens).

Coloration.—This is a species with exceedingly variable coloration. In general appearance these snakes are grayish, or brownish above, red or deep pink below, with three light marks on the occiput, and a light mark on the upper lip behind the eye.

The dorsal scales are uniformly pigmented with brownish or grayish and marked to varying degrees with chromatophore-like flecks of black. Specimens which seem grayish brown, on close examination are seen to have the brown ground color marked with blackish flecks; variation from "brown" to "gray" lies in the extent to which the blackish pigment flecks obscure the brown. Very dark gray specimens usually have the scales actually gray and much flecked with black. The skin between the scales is always black, but this is seldom apparent since the skin between the scales is not seen unless the body is distended as in females heavy with young. The dark flecks described above are usually not uniformly distributed over the dorsal scales, but tend to be aggregated on the scales of the first and sixth rows, resulting in dark longitudinal stripes of variable intensity. The skin between the fist and second scale rows is dotted with white, and the adjoining upper edge of the first scale row and the lower edge of the second scale row are narrowly tipped with white. Similar white flecks sometimes appear on the anterio-lateral edges of the more dorsal scale rows, particularly between the fifth and sixth rows and between the sixth and seventh rows. They are also sometimes present along the lower margin of the first scale row and the lateral edges of the ventrals. The white flecks are more frequent and somewhat larger on the lower scale rows and anteriorly. The posterior third of the body, the tail, and the median three dorsal scale rows usually do not have such white spots. The white is not superficially apparent, but in distended specimens, the white shows as stippled longitudinal lines.

This species is distinguished by the extension of the dorsal color onto the ventral plates. The dark coloration of the lateral margins of the ventrals is primarily due to the flecked, chromatophore-like black, rather than the uniform brown or gray ground color of the dorsal scales. Snakes that are brown above have the edges of the ventrals not brown but gray; those that are gray above have the change in coloratiion less obvious. In a few specimens, however, the only pigment edging the venter is the uniform ground color. In these there is a diffuse transition from the dorsal color to the clear red of the venter, rather than the sharp demarkation apparent in most. The gray of the edges of ventrals is often mixed with white, and this becomes particularly evident anteriorly, where white borders the margins of the ventrals, and the black pigment spots sometimes become confluent medially. As much as three-fifths of the belly may be obscured with dark leaving only a narrow central red band. The middle of the venter is normally bright red fading to white on the neck and chin shields, although some specimens from New York, New England, Pennsylvania, and elsewhere have the belly completely black. Since the red of the belly fades on preservation, most museum material has the belly white,

and it is impossible to say how much variation there is in this character. Corrington (1931) has reported a white bellied individual from Syracuse, New York.

The top of the head, like the scales of the body, is brown with a variable amount of black stippling, that generally begins at the level of the frontal plate and is sometimes so intense on the rear of the frontal and parietals that they appear black. The anterior portion of the head is lighter and brownish, lacking the dark speckling. The rostral is sometimes whitish. The sides of the head are similar, the plates before the orbit usually light brown, and those behind often heavily stippled and blackish. The upper labials, with the exception of the fifth, are similarly brown or whitish with variable amounts of black stippling mostly aggregated toward the rear of each scale. The last labial is often uniformly darkly pigmented. The greater part of the fifth labial is white, cream or pinkish. Most frequently the labial margin of the scale is stippled with black and there is a vertical black mark at the rear of the scale. The light color of this scale may reach the labial margin between these two dark marks, or it may be confined to the anterio-dorsal corner of the scale. In general, however, the mark is longer than high, and it never reaches the labial margin anteriorly. This marking thus differs from that of *S. occipito-maculata obscura*. The ventral part of the head, including the lower labials, mental and chin shields, is whitish, stippled with black.

The three occipital light spots, from which the species takes its name, are always present though with some variation in size and intensity. The lateral ones appear to be an anterior enlargement of the white stripe between the second and third scale rows, and are located directly behind the corner of the mouth. The median mark covers the occipital scales directly behind the suture between the two parietals. These spots may be reddish, orange, or whitish; they may be distinct, or only a little lighter than the ground color. The three spots are occasionally fused with one another to form a light bar on the neck. There is always some dark pigmentation on the lower scale rows or the edges of the ventrals separating the spots (or the light bar) from the clear venter, so that there is never a neck ring completely joined with the light venter as in *S. occipito-maculata obscura*.

Hemipenis.—The retractor penis muscle inserts at the level of the fourteenth to the nineteenth subcaudal. In dissecting the hemipenis the small distal spines are so fine that they cannot readily be distinguished from the severed muscle fibers. Thus the length of the penis itself could not be determined accurately. The insertion of the penis retractor muscle is abrupt and thus provides a convenient reference point.

The everted hemipenis is short and undivided, with the distal end expanded. The distal end is flattened and smooth, apparently without spines, but with densely placed fine spines around its edge. These become larger and more widely spaced proximally, but there are no much enlarged basal spines as in *S. dekayi*. The sulcus spermaticus arises medially, passes around the rear of the organ to the lateral side where it ascends to the tip in a relatively straight line.

Occasional specimens have a slightly enlarged basal spine, but these are from scattered parts of the range of this race, and the slight enlargement of this spine is of no apparent significance.

Dentition.—The dentition, determined from skulls of specimens from Ithaca, New York, and from maxillary and dentary bones of a few specimens from other localities, is as follows. The maxillary teeth are fourteen or fifteen in number. They are slender, slightly recurved, and subequal in length, except for the last two or three, which are about twice as heavy as the others. The dentary bears about seventeen teeth, gradually decreasing in length posteriorly, the anteriormost being the largest. The palato-pterygoid has thirty to thirty-three slender teeth that gradually decrease in length posteriorly.

Size.—The largest male examined was 359 mm. in total length (CM 17402 from Randolph County, West Virginia) and the largest female 383 mm., from Ithaca, New York. A summary by geographic regions, showing average length of mature individuals, maximum lengths, and tail/total length ratio is given in Table 5.

VARIATION

Scutellation.—The variation in ventrals and subcaudals is shown in Table 5. It is evident from this table that in any particular region the number of ventrals in the females exceeds that in the males, and that conversely the number of subcaudals in the males exceeds that of the females. The summary of the ventrals minus the subcaudals emphasizes the sexual difference in the ventrals and subcaudals.

An examination of Table 5 also shows that the number of ventrals tends to be less at lower altitudes, and toward the south. Specimens from New Jersey, Maryland, Virginia, and the Carolinas (where most of the specimens are from the coastal plain) and those from the Mississippi Valley and the Gulf Coastal Plain have lower counts than specimens from the north, and those from relatively high altitudes in the Appalachian area.

The highest subcaudal counts are found in the specimens from the lower Mississippi Valley, although as there are relatively few specimens available from that area it is not certain that this would hold for larger samples. The counts are also high in specimens from the northwestern periphery of the range of this subspecies. The lowest number of subcaudals is found in the north and east.

The ventrals are normally entire and the subcaudals divided, though with occasional abnormalities. A half scale may be interposed between the last ventral and the anal plate. Less frequently the last ventral plate is divided, or there is a half scale before the last ventral. A half scale may be interposed among the ventrals anywhere along the length of the belly. Entire subcaudals are rare, and usually less than half a dozen scutes near the base of the tail. A single specimen has the anal plate entire instead of divided, PA 1310, from St. Clair County, Missouri.

The variation in the plates of the head are summarized in Table 6. Variation from the normal six upper labials was found in 9.3 per cent of the specimens examined. The increase in labials from six to seven is accomplished by the splitting of the second labial, the last, or the next to the last. In those cases where the number of supralabials was reduced to five, the fusion was anterior to the orbit, that is, the second and the third labials fused to form a single plate. The lower labials are more variable than the upper, more than a quarter of all specimens examined (26.1 per cent) having an abnormality of one sort or another. The reduction in number of infralabials from seven to six is usually either the result of the fusion of the second and third, or the sixth and seventh. The reduction to five infralabials may be due to both these fusions occurring at once, or the fusion of the fifth, sixth, and seventh infralabials to form a single plate. Table 6 shows that fusions of this sort are much more frequent than splitting to form higher numbers of labials. Increase in number of infralabials is usually the result of splitting of the second or third labial.

Variation in number of preoculars and postoculars is also summarized in Table 6. It will be seen that there is great uniformity in the number of preoculars (only 4.3 per cent varying from the normal two) and a little more variation in the number of postoculars (6.6 per cent varying from the normal two). The posterior temporals show the greatest variation of all the head plates as they are other than 2/2 in 33.9 per cent of the specimens tabulated.

A loreal scale is present as an abnormality in several specimens. ROMZ 13 from Sudbury, Ontario, is provided with a loreal on each side and three other specimens, two from Ontario, and one from New York, had a loreal on one side only.

A single specimen, CLEM 225, from Clemson, South Carolina, has seventeen scale rows throughout the length of the body.

Coloration.—The normal range of color variation in this species is great. Many of the color forms have already been mentioned, and their composition discussed above (p. 22).

So-called melanistic specimens have been mentioned in the literature. Such specimens are not truly melanistic, but are merely blackish above, with the red of the belly replaced by black. These snakes have the prominent light occipital spots, and the fifth labial spot, and the chin is white and only flecked with black. The white flecks on the sides, forming longitudinal lines, are often unusually prominent. I have examined specimens from New York, New England and Pennsylvania, and various writers have reported them from elsewhere. M. Graham Netting, in an unpublished paper read at the April 1942 meetings of the American Society of Ichthyologists and Herpetologists, associates a greater frequency of snakes of this color phase with higher altitudes in West Virginia. In central New York they are found in certain localities while they are absent in other ecologically similar areas.

The black, chromatophore-like flecks that cover the dorsal scales to a greater or lesser degree are often wanting on the three median dorsal scale rows, so that while the sides are gray or even black, there may be a middorsal

TABLE 5.—Summary of Regional Variation in Certain Characters of *Storeria occipito-maculata occipito-maculata.*

	Northeast			North Central			Atlantic Coast			Upper Mississippi Valley			Gulf Coast		
		Extremes	Av.		Extremes	Av.		Extremes	Av.		Extremes	Av.		Extremes	Av.
Ventrals															
Males	(183)	114–129	119.1	(126)	112–132	120.5	(43)	110–124	116.2	(6)	110–115	113.0	(4)	117–122	118.8
Females	(197)	116–133	125.4	(142)	121–133	125.4	(32)	115–133	120.7	(7)	117–123	119.7	(14)	115–129	122.7
Subcaudals															
Males	(172)	43–58	48.9	(121)	42–55	49.3	(41)	42–59	48.7	(5)	46–54	48.8	(4)	51–61	56.2
Females	(187)	35–49	41.8	(135)	37–51	42.2	(30)	38–48	41.6	(7)	40–46	42.3	(12)	40–54	47.0
Ventrals + Subcaudals															
Sexes .... Combined	(359)	155–187	169.7	(255)	157–186	168.9	(71)	156–178	163.6	(12)	156–176	161.8	(16)	158–179	170.9
Ventrals — Subcaudals															
Males	(172)	64–82	72.8	(120)	61–82	71.2	(41)	60–74	67.4	(5)	57–67	63.8	(4)	57–71	62.5
Females	(187)	74–95	83.5	(135)	74–91	82.6	(30)	68–89	79.0	(7)	64–67	77.4	(12)	64–82	75.4
Total Length															
Males	(145)	359	242	(95)	347	238	(25)	281	215	(3)	214	202	(4)	278	182
Females	(139)	380	253	(105)	322	255	(26)	345	227	(5)	250	224	(10)	256	211
Tail/Total Length Ratio															
Males	(167)	21.1–26.6	22.8	(119)	21.0–27.7	23.6	(39)	24.2–27.0	24.5	(5)	20.8–28.6	24.8	(4)	25.3–29.8	26.6
Females	(183)	17.2–25.1	20.0	(131)	17.8–22.6	20.3	(30)	19.4–22.5	20.6	(7)	18.0–23.0	20.9	(11)	19.5–25.1	22.1

Figures contained in parentheses indicate number of specimens examined. For "Extremes" under "Total Length" only maxima are given. The average total length is derived from specimens over 175 mm. in length. (These are assumed to be mature.) Regions used may be outlined as follows: NORTHEAST—Quebec, New England, New York, Pennsylvania, and West Virginia; NORTH CENTRAL—Manitoba to Ontario south to Kentucky and Kansas; ATLANTIC COAST—New Jersey to Florida; UPPER MISSISSIPPI VALLEY—Arkansas, Missouri, and Tennessee; GULF COAST—Alabama to Texas.

TABLE 6.—Summary of Variation in Number of Head Plates in 730 Specimens of *S. o. occipito-maculata.*

Supralabials					5–R	5–L	5/5	6/6	7–R	7–L	7/7	
Frequency in per cent					1.4	1.5	1.2	normal	1.8	1.6	1.8	
Infralabials	3–R	4–R	5–L	5/5	6–R	6–L	6/6	7/7	8–R	8–L	8/8	
Frequency in per cent	0.6	0.1	1.0	0.1	5.1	7.4	7.5	normal	2.5	1.4	0.4	
Preoculars					1–R	1–L	1/1	2/2	3–R	3–L	3/3	
Frequency in per cent					0.4	0.7	0.6	normal	0.8	0.8	1.0	
Postoculars					1–R	1–L	1/1	2/2	3–R	3–L	3/3	
Frequency in per cent					1.5	1.4	0.7	normal	2.1	0.6	0.3	
Anterior Temporals								1/1	2–R	2–L	2/2	
Frequency in per cent								normal	0.1	0.1	0.1	
Posterior Temporals					1–R	1–L	1/1	2/2	3–R	3–L	3/2	4–L
Frequency in per cent					4.7	4.3	5.3	normal	8.8	6.3	4.4	0.1

band of brown, chestnut, or red. Occasionally the dark fleckings are absent from the first scale row as well as the median dorsal ones. Many specimens have the flecking much reduced or almost absent so that they appear brown or reddish since the ground color is not masked.

The shade of the belly color normally varies from pale pink to an intense bright red. There is no way of determining the shade of color in preserved specimens for in all the belly color fades to white with time, as is mentioned above. In my own experience with living specimens I have found no geographical correlation in this character.

HABITAT

This snake is found under logs and leaf mold in wooded areas, as well as under stones and boards in open fields. It is usually absent in densely populated areas, where *S. dekayi dekayi* and *S. d. wrightorum* are found in such abundance. At Ithaca, New York, they are not uncommon in the vicinity of buildings, providing good cover is available. The species has been thought to be nocturnal as its food is principally slugs, which feed at night. None of the writer's attempts to erect a distinction between the habitat of this species and that of *S. dekayi* have been successful. The two species have been found under adjoining stones. The general impression remains that *S. o. occipito-maculata* is a snake of more open places and greater altitudes.

DISTRIBUTION

Storeria o. occipito-maculata occurs from the Maritime Provinces and Quebec west to Manitoba, and south to Texas and central Georgia. The distribution over this vast area is characterized by a striking "spottiness." These snakes are locally common in many areas and surprisingly absent in other adjoining ones which seem similar in every respect. In central Georgia, extreme northwestern Florida, and adjoining portions of Alabama and Mississippi, this race intergrades with *S. occipito-maculata obscura*. There are but few reliable records from Texas where this must be accounted an exceedingly uncommon snake.

AFFINITIES

This race seems to be derived from *S. occipito-maculata hidalgoensis* which occurs to the south in Mexico. The coloration differences between the two races are distinctive but not profound, and it has been demonstrated that there is a gradual decrease in numbers of ventrals and subcaudals from *hidalgoensis* in the south to *occipito-maculata* in the north. The transition from subspecies *hidalgoensis* to *occipito-maculata* is not bridged by known intergrades, the area from which the transitional specimens might be expected being largely unsuited to these snakes, and the species here apparently persists in but small colonies. Were the differences between these two snakes more pronounced they might be considered specifically distinct.

LOCALITY RECORDS

Specimens examined as follows:

CANADA

MANITOBA: *Neepawa County*—Carberry, AMNH 9570; Douglas, CNM 960. *McDonald County*—Treesbank, CNM 1075, ROMZ 5306-09.

NOVA SCOTIA: *Annapolis County*—Annapolis Valley, North Mountain Road, CNM 1577; Spa Springs, CNM 1729. *Kings County*—Garland, CNM 1903. *Halifax County*—Hubbards on St. Margaret's Bay, CNM 1640. *Lunenburg County*—La Have Island, CNM 140. *Richmond County*—Cape Breton Island, St. Peters, CNM 1942. *Victoria County*—Cape Breton Island, Neil Hb., CNM 709.*Yarmouth County*—MCZ 6434; Central Argyle, AMNH 61585; Yarmouth, CNM 135.

NEW BRUNSWICK: *Charlotte County*—St. George, Lake Utopia, CORNELL 3413; near Grand Harbor, Grand Manan, MCZ 12668. *Northumberland County*—Chatham, CNM 1562. *York County*—Fredericton, ROMZ 4611-12. "Scotch Lake," CNM 1606, 1653, 1654; "New Brunswick," MCZ 317.

ONTARIO: *Algoma District*—Laird and vicinity, ROMZ 2905, 2909, 2904, 2907, 2899, 2902, 2903, 2895, 2893, 2906, 2896; Little Rapids, ROMZ 5377; MacLennan, ROMZ 2890, 2897-98, 2900-01, 2908, 3285-92; Sudbury, ROMZ 13; Georgian Bay, Tamarack Cove, Manitoba Island, UMMZ 74238; Georgian Bay, Cockburn, UMMZ 74240; Georgian Bay, Gore Bay, UMMZ 74239. *Bruce County*—Dorcas Bay, ROMZ 3825; Kinloss, ROMZ 4233. *Carleton County*—Ottawa, CNM 116, 150, 687, 781, 887, 895, 1033-34, 1133, 1135, 1285, 1737, 1777; Woodlawn, Constant Bay, Ottawa River, CNM 855. *Frontenac County*—ROMZ 2788, 3261; Arden, ROMZ 3395-96, 3819; Camp Oconto, ROMZ 3234-35; Buckshot Lake near Pierna, ROMZ 5347; Hartington, ROMZ 5044. *Haliburton County*—ROMZ 4020, 4030. *Huron County*—Clinton, ROMZ 2772; Lucknow, ANS 19714-16, 19718. *Muskoka District*—Sparrow Lake Camp, ROMZ 3090, 5305; Bracebridge, CNM 65, 73; Lake Rosseau, ROMZ 4752; Muskoka, Muldrew Lakes, ROMZ 5489; Port Sydney, ROMZ 5069. *Nipissing District*—North Bay, ROMZ 3895; Lake Timagami, ROMZ 2189; High Rock, Timagami, ROMZ 2369; Camp Otter, CORNELL 6686. *Ontario County*—ROMZ 3478, 3770, 2701-02, 2762; Gordon Bay, ROMZ 2799; Parry Sound, ROMZ 5364, 2790, 2859, 4983; Lake Nipissing, ROMZ 4679; Sequin Falls, Parry Sound, ROMZ 3478, 3770, 2701-02, 2762; Gordon Bay, ROMZ 2799; Parry Sound, ROMZ 4807-08. *Peterboro County*—Oak Lake, ROMZ 4680. *Renfrew County*—Arnprior, CNM 811. *Simcoe County*—Egbert, ROMZ 4728; Minesing, ROMZ 2807. *Timiskaming County*—New Liskeard, ROMZ 4581. *Victoria County*—ROMZ 3704; Cameron, ROMZ 5079; Coboconk, CNM 161, ROMZ 2616-17, 3719, 3720-22; Sturgeon Lake, ROMZ 4793. *York County*—Kelly Lake, ROMZ 4037; King Township, ROMZ 2239; Pottageville, ROMZ 96, 124, 182; Richmond Hill, ROMZ 5065; Toronto, ROMZ 20, 2320. "Lake Simcoe," ROMZ, 5082; "Ontario," ROMZ 2908.

QUEBEC: *Pontiac County*—Norway Bay, CNM 1151. *Quebec County*—Valcartier, Conway Lake, CNM 1991-92. *Sherebrooke County*—3 miles northeast of Sherebrooke, CORNELL 2367. *Wright County*—Aylmer, CNM 114, 786; Chelsea, CNM 82, 1469; Maniwaki, ROMZ 1818; Masham Mills, ROMZ 5434-35; Pink Lake near Hull, CNM 1435; Hull, CNM 685, 1132, 1564; Wakefield, CNM 948; Meach Lake, CNM 1426; Big Island, Blue Sea Lake, CNM 1662; Burbridge, CNM 1540, 1437; Whitefiish Lake, near Lucerne in Quebec, CNM 1735.

UNITED STATES

ALABAMA: *Jackson County*—Woodville, CM 7148-49. *Lee County*—near Auburn, UMMZ 83197, USNM 102586-87. *Mobile County*—Mobile, USNM 55790-91. *Sumter County*—near Bellamy, CM 9910.

ARKANSAS: *Garland County*—Hot Springs, Hot Springs National Park, FMNH 30873. *Lawrence County*—Imboden, KU 17162.

CONNECTICUT: Fairfield County—Stamford, AMNH 3388. *Litchfield County*—Norfolk, USNM 19972. *Tolland County*—Storrs, CORNELL 3499.

GEORGIA: *Rabun County*—Clayton, CORNELL 1392; Tallulah Falls, MCZ 9071. *Richmond County*—Augusta, USNM 8793. "Georgia," USNM 1912.

ILLINOIS: *Cook County*—CA 122; Braeside, FMNH 15698; Chicago, CORNELL 3408, USNM 6388; Evanston, MCZ 3274; Niles Center, FMNH 19317; Palos Park, FMNH 2972-73; Thatcher Woods, River Forest, FMNH 3289, CA 6106-08,

6176, 6725-88, 7923; Willow Springs, FMNH 19399. *DuPage County*—Forest Preserves, CA 6950-53, 6963-65. *Menard County*—Athens, MCZ 5523. *Richland County*—Olney, USNM 37973, 38415-18. *Saint Clair County*—Belleville, USNM 8772, 8775-76, 8990. *Union County*—7 miles west of Jonesboro, State Forest, FMNH 23716. *Wabash County*—Mt. Carmel, USNM 12022. "Bird Haven," USNM 49716; "Southern Illinois," USNM 7284; "Illinois," AMNH 2788; *Lake-Cook County* Line, west of Braeside, FMNH 22837.

INDIANA: *Brown County*—Game Reserve CM 9751, 9799-9800. *Knox County*—Wheatland, USNM 13359. *Lawrence County*—Twin Cave, Mitchell, UMMZ 61013. *Martin County*—Brown Township, CM 9738.

IOWA: *Clayton County*—Vicinity of Garnauillo, ISC 571-2, 577. *Dickinson County*—Lake Okoboji, UMMZ 52200. *Humboldt County*—three miles west of Ottosen, ISC 576.

KANSAS: *Douglas County*—Seven and a half miles southwest of Lawrence, KU 3581; Northwest of Lawrence, KU 7661. *Franklin County*—UMMZ 66982. *Hamilton County*—KU 2355. *Miami County*—CA 5277. *Phillips County*—Long Island, AMNH 3380. "Kansas," USNM 4657.

KENTUCKY: *Edmonson County*—USNM 55789; Jim Lee Ridge, KU 20098; near Mammoth Cave, USNM 1964, 79392; McBee Spring, MCZ 3512. "St. James," USNM 29643; *Hart* or *Edmonson County*, Mammoth Cave, AMNH 9631.

LOUISIANA: *Nachitoches Parish*—Creston, CORNELL, 7157, 7368, 7396; *Livingston Parish*—"Camp Wilson, Indiana Mound," FMNH 4809-10.

MAINE: *Androscoggin County*—Auburn, USNM 13716. *Cumberland County*—Portland, USNM 1935; Steep Falls, CORNELL 2667; Westbrook, USNM 17834. *Hancock County*—Brooklin, USNM 24065-93; Castine, USNM 17424; East Orland, SU 7778; Trenton, MCZ 719. *Kennebec County*—Vassalboro, MCZ 2351. *Oxford County*—Bethel, MCZ 723; Gilead, CORNELL 2548; Norway, MCZ 722, 2479. *Penobscot County*—Bangor, MCZ 332. *Waldo County*—Isleboro, ANS 3952, 3955, 5894. *Washington County*—twelve miles south of Calais, CORNELL 3178. "Lake Richardson," MCZ 716. *Piscataquis* or *Somerset County*, Moosehead Lake, AMNH 60025.

MARYLAND: *Calvert County*—Prince Frederick, USNM 76972. *Garrett County*—three miles east of Grantsville near Little Meadows, UMMZ 78247-48; near Lakewood M. E. Church, CORNELL 2809. *Montgomery County*—USNM 17562. *Queen Annes County*—Centerville, USNM 1937. *Worcester County*—Pocomoke State Park, CORNELL 3028; Old Furnace, CORNELL, 3029. "Maryland," MCZ 5907.

MASSACHUSETTS: *Barnstable County*—Woods Hole, USNM 37854, CM 16758, AMNH 2703. *Berkshire County*—Mount Washington, OUMZ R-487-1-5, R-487-7, 8, R-478, AMNH 58064. *Essex County*—USNM 55786. *Hampden County*—Chicopee, MCZ 5590. *Hampshire County*—Goshen, Road to Mt. Rest, CORNELL 469; Lake Norwich, OUMZ R-393; Worthington, MCZ 2358, 4792. *Plymouth County*—East Marshfield, OUMZ R-112. *Middlesex County*—Bedford, MCZ 2482; Cambridge, MCZ 724; Lexington, MCZ 17739; Sherborn, MCZ 2385; Waltham, MCZ 373, 380. *Worcester County*—Berlin, MCZ 744; Oxford, USNM 39287. "Massachusetts," ANS 5916.

MICHIGAN: *Baraga County*—Pequaming, ANS 19858. *Cheboygan County*—Douglas Lake, EMNH 26770, UMMZ 50125. *Chippewa County*—Brimley, OUMZ R-401; Whitefish Point, USNM 59733. *Clare County*—Tobaco River, UMMZ 74488. *Crawford County*—Higgins Lake, State Forest, UMMZ 72579. *Delta County*—Hunter's Creek, four miles north of Cornell, UMMZ 83762. *Emmet County*—Carplake, USNM 79332. *Grand Traverse County*—Arbutus Lake, UMMZ 64395. *Gogebic County*—Wakefield, USNM 51921-22; Bass Lake near Watersmeet, UMMZ 83766. *Houghton County*—USNM 55787. *Huron County*—Sand Point, UMMZ 37727-28, 74521. *Iosco County*—Van Etten Lake, UMMZ 82111-12. *Kalamazoo County*—ANS 12311. *Kalkaska County*—UMMZ 68830. *Keweenaw County*—Copper Harbor, ANS 5903-06,

5908-09, 5907 (TYPE Coluber venustus); Isle Royale, UMMZ 33408-17, 33475-76, 33478, 33493-94, 68838, 83875; Keweenaw Point, UMMZ 70198. *Livingston County*—Plainsfield, UMMZ 36159. *Luce County*—Pike Lake, UMMZ 61771. *Mackinac County*—St. Ignace, UMMZ 56324-25. *Macomb County*—Utica, UMMZ 72443. *Marquette County*—Huron Mountains, UMMZ 54061; Ishpeming, UMMZ 56691. *Mason County*—Bass Lake, UMMZ 56744. *Montmorency County*—UMMZ 62604. *Oakland County*—Franklin, UMMZ 66981; Lake Angelus near Pontiac, UMMZ 73218. *Otsego County*—Sturgeon River, UMMZ 64839. *Schoolcraft County*—Floodwood, UMMZ 47335. *Shiawassee County*—UMMZ 74536. *Washtenaw County*—Ann Arbor, UMMZ 74682; one mile east of Milford Road, UMMZ 82089. "Michigan," MCZ 720; "Northern Michigan," MCZ 5704.

MINNESOTA: *Clearwater County*—Itasca State Park near Lake Itasca, CM 20528. *Hennepin County*—Minneapolis, UMMZ 52511. *Rice County*—Northfield, CORNELL 3496. "Minnesota," MCZ 718; "Red River of the North," USNM 2133.

MISSISSIPPI: *Harrison County*—Biloxi, FMNH 21576, AMNH 46758, UMMZ 76824-25. *Wayne County*—seven miles north Waynesboro, USNM 99337.

MISSOURI: *Barry County*—Roaring River State Park, seven miles south of Cassville, CA 8643; Washburn, USNM 80987. *Carter County*—Current River, Big Spring State Park, UMMZ 68910. *Crawford County*—In USNM 55778-85 series. *Franklin County*—Meramec State Park, CA 8904. *Gasconade County*—Cooper Hill, CA 8513. *Jefferson County*—In USNM 55778-85 series. *Montgomery County*—In USNM 55778-85 series. *Oregon County*—In USNM 55778-85 series. *Ozark County*—In USNM 55778-85 series; CAS 17753. *St. Clair County*—seven miles northeast of Osceola, PA 950, 1310, 1348-49. *St. Louis County*—In USNM 55778-85 series. *Stone County*—Marble Cave, USNM 44293; vicinity of Marble Cave, AMNH 46820; in USNM 55778-85 series. *Wayne County*—Taskee Station, CA 8512.

NEBRASKA: "Eighty miles below Sargent's Bluffs," MCZ 135.

NEW HAMPSHIRE: *Carroll County*—Ossipee, USNM 44335. *Cheshire County*—Munsonville, AMNH 8689, 8789, 8933. *Grafton County*—Hanover, USNM 36012. *Merrimack County*—Franklin, MCZ 13799, 14158. *Hillsboro County*—Monadnock Mountain, altitude 2000 feet, USNM 52470, 52411. "Two miles from Upper Baker Pond," AMNH 49226.

NEW JERSEY: Burlington County—Atsion near route 39, CFK 89; Bear Swamp, ANS 15847; Friendship near Tabernacle, CFK 62; Mount Misery, CFK—. *Camden County*—West Berlin, ANS 21505. *Cumberland County*—Vineland, CFK 122, 128, 142, 143. *Middlesex County*—Spottswood, AMNH 43917. *Ocean County*—Lakehurst, AMNH 38177; Lakewood, Lake Carosaljo, UMMZ 78946; Lakewood, CORNELL 1274; West Lakewood, CORNELL 1273; Stafford's Forge, ANS 18647. *Passaic County*—Moe, AMNH 43916.

NEW YORK: *Cattaraugus County*—Allegany State Park, URMNH 4186, 6616; Olean, AMNH 46081, 46104-5, 60204-16, 60218-21. *Chautauqua County*—one mile from Chautauqua, URMNH 5657-5666; one-half mile north of Panama, URMNH 4140. *Clinton County*—six miles southwest of Peasleeville, USNM 82548-49. *Cortland County*—McLean, CORNELL 1039, 1870, 2531; just northeast of Chicago Bog, CORNELL 2192. Delaware County—two miles northeast of Downsville, UMMZ 78947. *Erie County*—Eden, CORNELL 3205; Hamburg, CORNELL 1391. *Essex County*—ANS 18970-71; Keene Valley, USNM 16690; near Severance, AMNH 32894-97. *Genessee County*—Bergen Swamp, URMNH 3146-47, CORNELL 2187. *Hamilton County*—ANS 5920; Blue Mountain, URMNH 6596. *Herkimer County*—one-half mile southeast of Poland Center, URMNH 4139; Poland Center URMNH 4144. *Jefferson County*—Philadelphia, CORNELL 3505; Watertown, URMNH 2016. *Madison County*—Peterboro, USNM 28361-63. *Monroe County*—Rochester, URMNH 2176, 2729-30, 3142-45, 3593, 4193; Union Hill, URMNH 3431. *Onondaga County*—Syracuse, USNM 76135. *Orange County*—FMNH 2030; Palisades Inter-State Park, Lake Tiorati, CORNELL 923; Greenwood Lake, AMNH 6715-18; West Point, AMNH 3390. *Orleans County*—Quarry near Albion, URMNH 1173. *Otsego*

County—Oneonta, ANS 5901-02. *Queens County*—Long Island, Flushing, AMNH 59712-13, 59720. *Rensselaer County*—Berlin, USNM 82550. *St. Lawrence County*—Madrid, USNM 1939. *Schuyler County*—Cayuta Gorge, CORNELL 1922. *Steuben County*—Addison, URMNH 6661; two miles west of Kanona, CORNELL 2196; one mile west of North Cohocton, CORNELL 2254. *Suffolk County*—Lake Grove, USNM 44360; Long Island, Mt. Sinai, AMNH 20631, 4157; Long Island, Wading River, Camp Wauwepex, CM 2689-90. *Sullivan County*—ANS 5895; seven miles north of Monticello, UMMZ 78945; Neversink, URMNH 2157. *Tioga County*—ANS 5915; Berkshire, MCZ 254, 374; three-fourth of a mile southeast of Lockwood, CORNELL 2386; Prospect Valley near Willseyville, CORNELL 3241, 2375, 1306; Spencer, CORNELL 1850. *Tompkins County*—Ithaca, CORNELL 1123, 1204, 1319, 1378, 1908, 2278, 2282, 3030, 3123, 6094, 6999, 7012, 7061, 7069-73, 7075, 7082, 7550, 7045, 2289; McLean, CORNELL 1856; above Taughannock Falls, CORNELL 3210; Turkey Hill near Varna, CORNELL 3239; Cortland Road north of Varna, CORNELL 1293; West Danby, CORNELL 3232. *Warren County*—two miles west Creek Center Post Office, USNM 82547; Lake George, USNM 80318. "Long Island," AMNH 3391-95; "Catskill Mountains, Slide Mountain," CORNELL 3280; "*Ulster or Greene County*, Catskills," USNM 23143-45.

NORTH CAROLINA: *Avery County*—Cranberry, ANS 4779-80, 4789-90, USNM 16264; Pineola, AMNH 8416. *Buncombe County*—Swannanoa, UMMZ 76427. *Catawba County*—Catawba, MCZ 4313. *Harnett County*—Summerville, USNM 2146. *Haywood County*—Sunburst, ZSP 387. *Henderson County*—Hendersonville, CHM—. *New Hanover County*—Wilmington, SUMNH. *Wake County*—Raleigh, SUMNH 1739, CM 5584, FMNH 2031, 22758-59. "Chubb Gap, Pisgah Forest," UMMZ 52680; "Natahala National Forest, near Ravenel Lake," USNM 104526.

NORTH DAKOTA: *McHenry County*—Towner, MCZ 37195. "*Bottineau* or *Rolette County*, Turtle Mountains," UMMZ 54473.

OHIO: *Butler County*—Hughes, USNM 10089. *Franklin County*—Columbus, ANS 6463. *Lake County*—Madison, USNM 6473. *Mahoning County*—Yellow Creek, Poland, USNM 2151.

PENNSYLVANIA: *Allegheny County*—Pittsburgh, USNM 1938; Wilkinsburg, CM 4769. *Bedford County*—near Everett, CM 5387. *Blair County*—CM 14585. *Bradford County*—near Troy, CM 6171. *Bucks County*—Near Langhorne, Meshaming Creek, ANS 21507. *Butler County*—Near Forestville, LMK 21474; Slippery Rock, near Wolf Creek, CM 8096. *Cambria County*—Flynton, CM 1285; Lloydsville, CM 2050. *Carbon County*—Hickory Run Recreation Area, AMNH 62906. *Center County*—MCZ 2396; ten miles west of Milroy, Seven Mountains, CM 5267-69; Ingleby, CORNELL 2195; Osceola Mills, CM 6681. *Clarion County*—Strattonville, CM 1115. *Clearfield County*—Clearfield, CM 8847. *Clinton County*—Honeyville to Williamsport, CM 1348; Henryville, CM 1354; Keating, CM 8843; Round Island, ANS 4614; Sproul Forest plateau south of Keating, CM 12719-21. *Crawford County*—Near Linesville, Hemlock Island, CM 7643, 11465. *Elk County*—Clover Hill Farm, CM 13497-99, 19983-84; Johnsonburg, ANS 14536; two miles south of Wilcox along Clarion River, CM 19250. *Fayette County*—Ohiopyle, ANS 17720. *Forest County*—Brookston, CM 12999; near Cooksburg between Cook Forest and National Forest, CM 5360; Cook Forest, CM 17318. *Fulton County*—Amaranth, CM 8834. *Huntington County*—Diamond Valley, ANS 16599. *Jefferson County*—Near Brookville, Baxter, CM 6643. *Lackawanna County*—Moscow, ANS 18968-69. *Lycoming County*—Cammal, ANS 22023. *McKean County*—Bradford, CORNELL 1393-94. *Mercer County*—cne mile north of Mercer, CORNELL 3422. *Mifflin County*—Near Milroy, CM 6188. *Monroe County*—Near Cresco, ANS 3950-51; Mt. Pocono, ANS 15966; Pocono Lake, ANS 17706. *Philadelphia County*—Chestnut Hill, ANS 14728. *Pike County*—Six miles south of Porter's Lake, CM 9704-06. *Potter County*—Near Inez, CM 5123; Stewardson Township, ANS 13992. *Somerset County*—Laurel Ridge near Jennerstown, CM 780; three miles east of Stoystown near Lincoln Highway, CM 10592. *Sullivan County*—Ganoga Lake, ANS 12418-19; three miles east of Lopez, CM 6257; Shady Nook, ANS 20867. *Warren County*—Near Pine Valley, Tamarack Sw., near Sulphur Spring, CM 7086-93, 7734; near Scandia, UMMZ 68669. *Westmoreland County*—Near Waterford, Pine Hill, CM 4881-82, CM 4884; near New Florence, three miles from

Twin Echo, CM 5199. *Wyoming County*—Bella Sylva, ANS 14970. "Camel," ANS 19603.

SOUTH CAROLINA: *Anderson County*—Anderson, USNM 1917, 2144, MCZ 5906. *Beaufort County*—three miles northwest of Sheldon, CA 10872. *Berkeley County*—Alvin, S-M 194-105, 201-106, 202-107. *Charleston County*—Charleston, MCZ 27-28, 114. *Darlington County*—Society Hill, USNM 2147. *Lexington County*—Five miles southeast of Leesville, CM 9530. *Oconee County*—Clemson College, CLEM 215, 225. *Pickens County*—Rocky Bottom, CLEM 174, 211, CHM 30-173-3. *Richland County*—Columbia, CHM 31-219-16. "South Carolina," CLEM 216.

SOUTH DAKOTA: *Pennington County*—Hill City, USNM 17640.

TENNESSEE: *Decatur County*—Perryville, KU 2471.

TEXAS: "Texas," MCZ 299, 715. Obviously E. Texas.

VERMONT: *Addison County*—Granville, AMNH 63528-29; Hancock, AMNH 60217, 63510-12, 63514-18, 63623. *Caledonia County*—St. Johnsbury, USNM 40100. *Essex County*—Lunenberg, MCZ 2304 (one hundred and six specimens); Miles Pond, AMNH 7757. *Lamoille County*—Stowe, AMNH 38178, USNM 103304-6; two and one-half miles west southwest Stowe, USNM 108705; four miles northeast Stowe, USNM 108715. *Washington County*—Nichols Pond, CORNELL 2555; Northfield, AMNH 46249; Roxbury, CA 339-44.

VIRGINIA: *Augusta County*—O'Connell's Farm, USNM 36737. *Fairfax County*—Near Burke Station, USNM 110953; Mt. Vernon, USNM 29622. *Henry County*—Spencer, CM 13962; *New Kent County*—Near Lanexa, CM 18581. *Pittsylvania County*—Danville, MCZ 13061-62.

WEST VIRGINIA: *Grant County*—Near Dorcas, CM 5382. *Hampshire County*—Near Romney, CM 6130. *Lincoln County*—Branchland, CM 18071. *McDowell County*—two miles south of Panther, CM 15946. *Nicholas County*—Near Richwood, CM 12000. *Pocahontas County*—Cranberry Glades, CM 11981, 12037. *Preston County*—Snaggy Mountain, CM 15570; near Terra Alta, CM 6079, 6137, 6946. *Randolph County*—Near Elkins, CM 15612, 15649; one mile above Elkwater, CM 9588; Gardineer Knob, CM 17401-03; near Huttonsville, CM 8441. *Tucker County*—Canaan Valley, CM 6966-67; Coketon, CM 9945. *Webster County*—near Dyer, CM 12010. *Wyoming County*—One and one-half miles south of Pineville, CM 15891. "West Virginia," CM 15611.

WISCONSIN: *Ashland County*—Bear Lake, FMNH 18434. *Bayfield County*—Twin Lake Camp Iron River, UMMZ 74552-54. *Clark County*—Dewhurst Township, FMNH 14596-99, 14601; Thorp Township, FMNH 14605; Hewett Township, FMNH 13046-48; Mentor Township, FMNH 14602-3; Worden Township, FMNH 5533, 8079, 8257-58, 8296-97, 12680-83, 14594-95, 14600, 14604, 14606-09, 14795-97. *Iron County*—UMMZ 58589. Jackson County—Millston, FMNH 19214. *Langlade County*—Ainsworth Township, Mosquito Lake, CA 3834-43, 5478. *Marathon County*—Trapp River, UMMZ 64745. *Marinette County*—Coleman Lake, FMNH 3312. *Oconto County*—Bear Paw Lake near Little James Mountain, FMNH 29370. *Oneida County*—Big Fork Lake, Three Lakes, FMNH 26045; twelve miles northwest of Rhinelander, CA 6821-7; four miles southeast of Rhinelander, CA 6828. *Racine County*—Racine, USNM 7281. *Sauk County*—Baraboo, USNM 10715. *Shawano County*—Red River, CA 6829-33, 6837, 6838-52. *Taylor County*—seven miles north of Medford, UMMZ 69625. *Vilas County*—USNM 55788, OUMZ R-226, 227, 228; Lake Mishishe, FMNH 22892-93. "Upper Wisconsin," USNM 7280.

Storeria occipito-maculata obscura Trapido, subsp. nov.

Florida Red-bellied Snake

Figs. 14-20

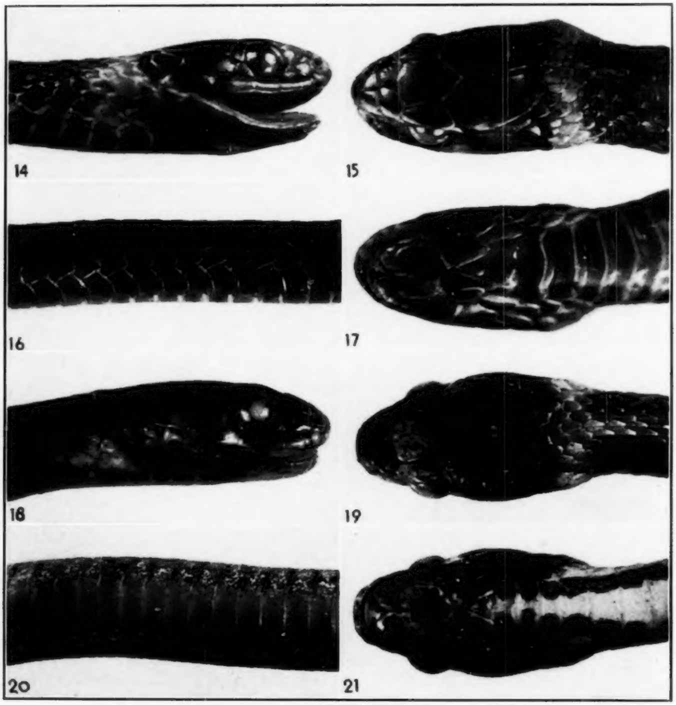
Storeria occipitomaculata Cope, Proc. Amer. Philos. Soc., vol. 17, p. 64, 1878.

Storeria occipito-maculata Cope, Proc. U. S. Nat. Mus., vol. 11, p. 391, 1888; Loennberg, Proc. U. S. Nat. Mus., vol. 17, p. 333, 1894; Wright and Bishop, Proc. Acad. Nat. Sci. Phila., vol. LXVII, p. 178, 1915; Van Hyning, Copeia (1), p. 6, 1933; Stejneger and Barbour, Check List N. Amer. Amph. Rept., Ed. 4, p. 131 (partim), 1939; Carr, Univ. Fla. Pub. Biol., Sci. Ser., vol. 3, p. 91, 1940.

The citations above appear to be the only ones definitely referable to *S. occipito-maculata obscura.* This new race is apparently not common, and it is only after the examination of relatively recent collections that diagnosis is possible.

DESCRIPTION

Diagnosis.—Characters of *S. o. occipito-maculata* but differing as follows: the top and sides of the head are black, with the occasional exception of the portion before the eyes and the anterior portion of the fifth supralabial which is white to the lower margin of the scale. The anterior tip of the first labial is also sometimes white. The occiput is marked with a light ring about two scales



Figs. 14-21. All figures somewhat enlarged. *Storeria occipito-maculata obscura,* FMNH 8561, Holotype, from Gainesville, Florida. Fig. 14. Lateral view of head and neck. Fig. 15. Dorsal view of head and neck. Fig. 16. Lateral view of body. Fig. 17. Ventral view of head and neck. *Storeria occipito-maculata obscura.* Fig. 18. Lateral view of head and neck. Fig. 19. Dorsal view of head and neck. Fig. 20. Ventral view of body. Fig. 21. Ventral view of head and neck. *Storeria o. occipito-maculata* from Ithaca, New York.

in width, joining the light color of the venter laterally. The dorsal body color varies from light tan to black. Ventrals fewer, and subcaudals more numerous than in *S. o. occipito-maculata*.

Holotype. — FMNH 8561, adult female, Florida, Alachua County, Gainesville, October 1922. Collected by T. Van Hyning.

Scutellation of Holotype.—Dorsal head plates normal, prefrontals a little larger than the internasals; nostril contained within anterior nasal; posterior nasal slightly larger than anterior, separated from the anterior nasal below, but not above the nostrils; preoculars two, the upper larger; postoculars two, the upper larger; anterior temporal single, about twice as long as high; posterior temporals two, the lower larger; supralabials six, the fifth and sixth largest, others in descending order of size, four, three, one, two; most of the fourth and the rear of the third entering the orbit; infralabials seven, the fifth largest, others in descending order of size, four, six, one, seven, three, two, the first labial of each side meeting its mate of the opposite side behind the mental; chin shields in two pairs, the anterior longer than the posterior, both pairs somewhat torn in the holotype, a single scale separating the rear two-thirds of the posterior chin shields; dorsal scales in fifteen rows throughout, keeled, emarginate posteriorly, apical pores not apparent, first scale row about half again as wide as others, somewhat more weakly keeled; ventral scales 116; anal plate divided; subcaudal scales in 42 pairs; total length 260 mm., tail 54 mm.

Coloration of Holotype.—The specimen was probably somewhat darkened in preservation, but the coloration is as follows: head black above to the rear of the parietals, a little lighter on the internasals; black laterally except for the anterior two-thirds of the fifth supralabial which is white, with some weak, faint dark stippling, and the anterior portions of the first and second supralabials which are somewhat lighter; black extending posterior to the first scales behind the posterior temporals, and extending ventrally to cover the last two infralabials, and portions of the others; white neck ring two scales wide at the level of the rear of the parietals, but not extending onto the parietals; all dorsal body scales black, with no evidence of any marks; venter white in alcohol (probably red or pink in life), with the black of the dorsum extending onto the lateral edges of the ventrals for a distance about equal to the width of the first scale row.

Hemipenis.—The description of the hemipenis is based on an examination of several specimens other than the holotype, which is a female. The penis retractor muscle inserts at the level of the seventeenth subcaudal scale. In general features, such as the somewhat expanded distal end, the location of the sulcus spermaticus, and the nature of the spines, the hemipenis of subspecies *obscura* is like that of *S. o. occipito-maculata*. One of the specimens examined had a somewhat enlarged spine at the base of the organ and to one side of the sulcus, but such an enlarged spine is not constantly present. This spine is not so pronouncedly enlarged as is the case with the basal spine in the hemipenis of *S. dekayi*, but it is noticeably larger than its fellows.

Dentition.—The teeth are largest anteriorly, and become gradually shorter toward the rear. A specimen from the Okefinokee Swamp, apparently has twelve teeth on the dentary, but the jaw is broken.

Size.—The largest male from Florida is 215 mm. in total length (four specimens), the largest female 260 mm. (five specimens). The largest male from Georgia is 197 mm. in total length (three specimens), the largest female 231 mm. (five specimens). A summary of the average total length and the tail/total length ratio is given in Table 7.

VARIATION

Scutellation.—Variation in scutellation is summarized in Tables 7 and 8. A comparison of the average number of ventrals with those of *S. o. occipito-maculata* (Table 5) shows that subspecies *obscura* has a lower number of ventrals. The sexual dimorphism in subcaudal counts is pronounced. Since the increase in subcaudals balances the decrease in number of ventrals, the sum of the ventrals and subcaudals in *S. o. obscura* approximates that of *o. occipito-maculata* from localities to the north. The average for seventeen specimens, males and females combined, is 165.9. The high number of subcaudals and the low number of ventrals is reflected in the figures given for the ventrals minus the subcaudals, which average lower in *obscura* than in *occipito-maculata* from the north.

The variation in head plates is shown in Table 8. There are no abnormalities recorded for the infralabials, preoculars, or anterior temporals. The number of posterior temporals may be increased from two to three. The head scutellation in this subspecies seems remarkably stable.

All specimens examined had fifteen scale rows. The first scale row may be as strongly keeled as the others, or the keels may be somewhat weaker. The margination at the rear of the scales of the first row is lacking in some specimens.

Coloration.—Most of the specimens have the body scales a light brown, tan, or reddish, with the head, in striking contrast, black. Other specimens, like the holotype and CORNELL 7189, have the body fully as dark as the head. In body coloration the range of variation will probably be found to be as great as in subspecies *occipito-maculata*. On lighter specimens there is usually a series of fine dots along the sixth scale row, tending to form a longitudinal line. Similar flecks of pigment are also sometimes present on the first scale row. Subspecies *obscura* has the dorsal color extending onto the edges of the ventrals for a distance equal or a little greater than the width of the first scale row. In the specimens with the dorsum blackish, the pigment is of the same intensity on edges of the ventrals, as above, and there is a rather sharp line of demarkation between it and the clear belly. The snakes with the lighter colored back may have only this tan pigment bordering the outer edge of the ventrals (UMMZ 58549, 79577), or there may be an intensification of the pigment due to the accumulation of flecks of dark grey or black, so that there appears to be a black line on each side adjoining the outer edge of the ventrals (CORNELL 6238, 7190). These black lines are not along the edges of the

TABLE 7.—Summary of Regional Variation in Certain Characters of *Storeria occipito-maculata obscura.*

	Males			Females		
	No.	Extremes	Average	No.	Extremes	Average
Ventrals						
Florida	4	114-116	114.7	7	111-126	119.1
Georgia	3	113-116	115.0	6	116-124	120.1
Subcaudals						
Florida	4	46-56	50.8	5	42-48	44.6
Georgia	3	49-57	52.5	5	44-49	46.6
Ventrals-Subcaudals						
Florida	4	62-68	64.0	5	63-84	75.0
Georgia	1	59-67	62.6	5	70-80	74.4
Total Length						
Florida	3	215	199.7	5	260	212.8
Georgia	1	197	197.0	3	231	203.6
Tail/Total Length Ratio						
Florida	4	25.1-27.2	26 2	5	20.8-21.8	21.5
Georgia	3	24.8-26.4	25.7	5	21 2-23 7	22 6

TABLE 8.—Summary of Variation in Head Plates in 19 Specimens of *S. occipito-maculata obscura.*

Supralabials		5–L	6/6
Frequency in per cent		5.3	normal
Preoculars		3/3	2/2
Frequency in per cent		5.3	normal
Posterior Temporals	3–R	3–L	2/2
Frequency in per cent	5.3	21.0	normal

ventrals, but set in a short distance from the margins, which are tan like the back. The latero-ventral black stripes become faint posteriorly and are wanting on the tail, but anteriorly they are well defined and run into the dark pigment of the posterior lower labials and adjoining scales. It may be presumed that the belly is pink or reddish in life.

The occipital light ring of this race is a modification of the three light occipital spots of typical *occipito-maculata.* Some specimens have the ring uniformly one and a half or two scales wide, while others have broader areas laterally and medially, in the position of the light occipital spots of subspecies *occipito-maculata,* narrowing to one scale in width at the level of the sixth scale row, where typical *occipito-maculata* would have the ring interrupted by the darker ground color. In the specimens examined, the light neck ring is either directly behind the parietals, or separated from them by only one scale. Typical *occipito-maculata* may very rarely have the three occipital spots fused with each other, but the resulting light bar does not reach the light ventrals.

The blackening of the head, characteristic of *obscura,* is subject to some variation on the underside. The material from Okefinokee Swamp (CORNELL 7189-90, 6328) has the chin shields and infralabials, and the scales directly behind them completely black, while specimens from north central Florida have the chin shields and infralabials anterior to the fifth merely spotted with black. These agree with the Okefinokee material in having the

infralabials posterior to the middle of the fifth, and the scales behind, completely black. In all specimens the tip of the snout is lightened. Thus the rostral itself is not black, and the mental is either whitish, or with only a black posterior margin. Some specimens (AMNH 7463, 8334, 38353) are light posteriorly to the level of the middle of the frontal.

The light mark on the fifth labial, characteristic of the several races of *occipito-maculata*, differs in *obscura* in that it is not interrupted along the lower margin, as in typical *occipito-maculata*. Specimens from southern Georgia and two from Florida (AMNH 7463 and 8334), have black obscuring all but the anterior fourth of the scale, and a little of the posterior margin of the preceding scale, while snakes from Florida have three-fourths of the scale whitish. The anterior tip of the first supralabial may also be light.

These coloration characteristics, when taken together provide a ready means of distinguishing the red-bellied snake of peninsular Florida and the adjoining portions of northern Florida and the coastal plain of Georgia.

At the periphery of the range of *obscura*, i.e., in the panhandle of Florida and in western Georgia, specimens are found with the head coloration as described above, but with the occipital spots not fused to form a neck ring. Such snakes are regarded as intergrades between the typical subspecies *occipito-maculata* and subspecies *obscura*. Similarly modified specimens have also been seen from further west along the Gulf.

HABITAT

Very little has been written on this snake. We do know that it is decidedly uncommon. Carr (1940) found it fossorial, burrowing in leaf mold, and under bark and logs. He found two in piles of debris at the bases of magnolia trees.

DISTRIBUTION

S. occipito-maculata obscura ranges from Pasco and Volusia counties in Florida north and west to Jefferson Country, Florida, and Monroe County, Georgia; i.e., from central Florida north onto the coastal plain of Georgia. Mr. E. Ross Allen records red-bellied snakes from Sarasota and Charlotte counties in southern Florida, but these records require confirmation. The specimen from Monroe County, Georgia, is at the edge of the coastal plain, but is undoubtedly of this race.

AFFINITIES

The Florida red-bellied snake is obviously closely related to the widespread northern form. The genus *Storeria* has two endemic forms in the Floridian region, *S. victa* and *S. occipito-maculata. obscura*. *S. victa* presumably developed during the period of isolation of a *Storeria* on a tertiary Floridian island or group of islands, and *S. occipito-maculata obscura* evolved during the recent invasion of the reunited area by *S. occipito-maculata*. Whatever forces have produced the tendency toward differentiation in the recent herpetofauna of Florida, have molded subspecies *obscura* from *S. occipito-maculata*. The differences between subspecies *obscura* and *occipito-maculata* are of the same

order as those in *Lampropeltis getulus, Natrix cyclopion, Tantilla coronata, Micrurus fulvius,* and others in this same area.

LOCALITY RECORDS

Specimens examined as follows:

FLORIDA: *Alachua County*—UMMZ 58549; Gainesville, UMMZ 79577, AMNH 3397, FMNH 8561 HOLOTYPE; Waldo, FMNH 8562; San Pulaski (San Felasco) Hammock, UFC 348. *Jefferson County*—Monticello, ERA 47-A. *Marion County*—Eureka, AMNH 7463, 8334; Silver Springs, CORNELL 3432; Hull Lake, ERA 47-B. *Pasco County*—Argo, ANS 12308. "Florida," ANSP 12305.

GEORGIA: *Charlton County*—Billy's Island, Okefinokee Swamp, CORNELL 6238, 7189-90; Floyd's Island, Okefinokee Swamp, AMNH 38353. *Grady County*—Sherwood Plantation, fifteen miles west of Thomasville, CA 9221-2. *McIntosh County*—two miles east of Eulonia, CM 15340, 16614. *Monroe County*—four miles north of Culloden, CM 17881.

Also recorded as follows:

Escambia County—(Carr, 1940).

Marion County—Oklawaha River, ten miles southeast from Ocala (Loennberg, 1894).

VOLUSIA: "Volusia" (Cope, 1888).

Intergrades between *Storeria occipito-maculata occipito-maculata* and *obscura* examined as follows:

FLORIDA: *Gadsden County*—three miles southeast of River Junction, UMMZ 86468. *Jefferson County*—near Monticello, UFC 630.

GEORGIA: *Baldwin County*—Milledgeville, MCZ 285. *DeKalb County*—MCZ 31854. *Fulton County*—Roswell, MCZ 12787. *Grady County*—15 miles west of Thomasville, Sherwood Plantation, CA 5186. *Rabun County*—Mountain City, near Wilson Gap, CORNELL 6359. "Georgia," MCZ 275.

MISSISSIPPI: *Greene County*—Gaine's Creek, URMNH 4206.

SOUTH CAROLINA: *Oconee County*—five miles west of Jocassee, CM 17733.

STORERIA VICTA Hay

Florida Brown Snake

Figs. 22-25

Storeria dekayi Loennberg, Proc. U. S. Nat. Mus., vol. 17, p. 332, 333, 1894; Brimley, Proc. Biol. Soc. Wash., vol. 23, p. 15 (partim), 1910; Wright and Bishop, Proc. Acad. Nat. Sci. Phila., p. 177, 1915; Deckert, Copeia, No. 54, p. 32, 1918.

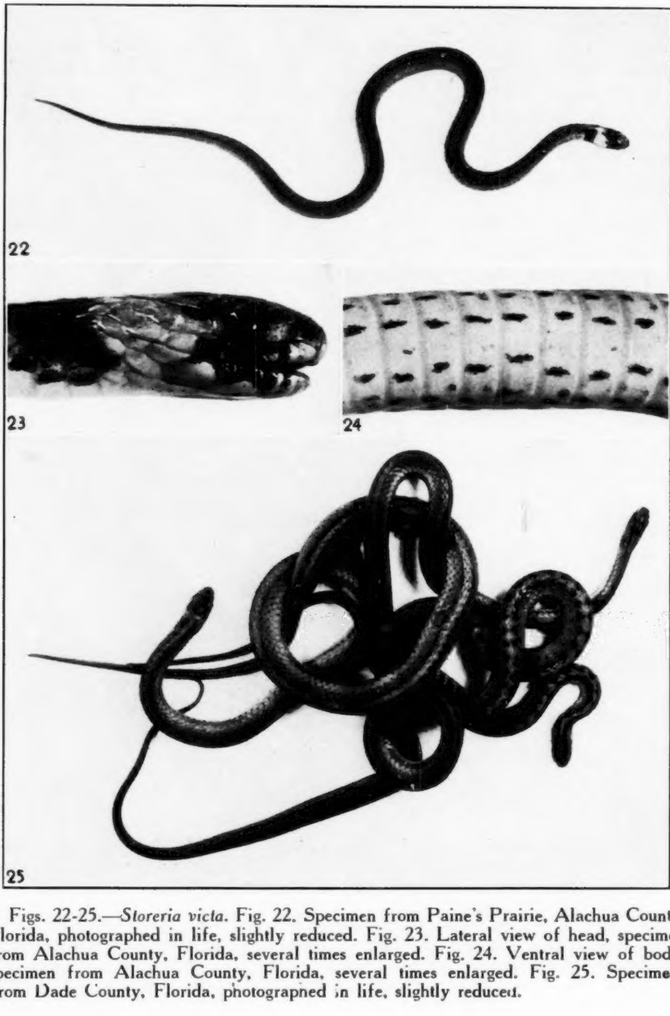
Ischnognathus victa Boulenger, Cat. Snakes Brit. Mus., vol. 3, p. 611, 1896.

Storeria victa Hay, Science, vol. 19 (479), p. 199, 1892; Stejneger and Barbour, Check List N. Amer. Amph. Rept. Ed. 4, p. 131, 1939; Carr, Univ. Fla. Pub. Biol., Sci. Ser., vol. 3, p. 90, 91, 1940.

This species was described from a specimen found in the alimentary canal of a coral snake (*Micrurus fulvius*) taken on the bank of the Oklawaha River "some distance north of Kissimee, Florida." *Storeria victa* was distinguished from *S. dekayi* by the number of dorsal scale rows (fifteen instead of seventeen), the greater proportional width of the scales, the greater number of ventrals (146) and the presence of two rows of spots on the ventral scales. Loennberg (1894) identified a snake of this species from Kissimee as *S.*

dekayi. As recently as 1940, Carr implied that *victa* will be found to intergrade with *dekayi* in northern Florida and southern Georgia, so that *victa* would become a race of *S. dekayi*. I find no evidence, however, that *S. victa* intergrades with any of the forms of *dekayi*.

While Hays (1892) stated that he intended to place the type of this



Figs. 22-25.—*Storeria victa*. Fig. 22. Specimen from Paine's Prairie, Alachua County, Florida, photographed in life, slightly reduced. Fig. 23. Lateral view of head, specimen from Alachua County, Florida, several times enlarged. Fig. 24. Ventral view of body, specimen from Alachua County, Florida, several times enlarged. Fig. 25. Specimens from Dade County, Florida, photographed in life, slightly reduced.

species in the United States National Museum, the specimen is not now there, and Dr. Stejneger informs me he has no recollection of its having ever been deposited.

DESCRIPTION

Diagnosis.—Scales in fifteen rows, head plates normally as in *S. dekayi.* Ventrals and subcaudals high in number. Dorsal color brown with dark spots of varying intensity on the sixth scale row. Belly whitish, variously marked with dark flecks laterally, or almost unmarked. Head characteristically with a light band posteriorly, followed by a dark band on the occiput, labials below the orbit dark.

Scutellation.—Dorsal head plates normal; anterior nasal usually subequal to posterior, higher than long, fused or separate from the latter; posterior nasal about equilateral, or slightly higher than long; preocular normally entire, twice as high as broad; supraocular twice as long as wide; postoculars normally two, narrow, the upper usually slightly the larger; anterior temporal single; posterior temporals normally two; upper labials seven, the third and fourth entering the orbit, the seventh largest; lower labials normally seven, the fourth and fifth much larger than the others, the first pair in contact between the mental and the anterior chin shields; mental triangular, broader than long; chin shields in two pairs, subequal in size, in contact medially, the rear third of the posterior pair separated by a small scale.

Ventrals in males 131 to 142 (sixteen specimens), in females 130 to 148 (thirty-three specimens); anal plate divided; subcaudals divided, in males 52 to 69 (fourteen specimens), in females 46 to 64 (twenty-two specimens).

Coloration.—The head and body brown; scales of the top of the head peppered with black to varying degrees. The labials lighter, straw to whitish, except the third to fifth supralabials and the adjoining margins of the lower labials, which are usually black and always somewhat darkened. Usually some black on the postoculars and the forward portion of the anterior temporal. A light band, actually white in some specimens. usually present on the rear of the head, from the rear of the anterior temporal to a little behind the angle of the mouth. Behind this, on the occiput, a dark band, usually three scales wide, narrowing or interrupted on the middorsal line, extending laterally and ventrally to the margins of ventrals. Body scales brown or tan with a variable amount of black flecking on the scales of the sixth row. Occasional specimens with this flecking intensified and involving the adjoining scale rows, and occasional joining of the spots across the back to form short bars as in *S. dekayi wrightorum.* Usually some slight encroachment of the dorsal ground color onto the tips of the ventrals. A light vertebral band on the median three scale rows sometimes evident. Belly whitish, and often with a spot on each end of each ventral; markings often scattered on the ventrals as in *S. dekayi;* occasional specimens almost unmarked on the belly.

Hemipenis.—The penis retractor muscle inserts at about the level of the twentieth subcaudal, the organ itself reaching to about the eighth subcaudal. In the organ dissected *in situ*, the sulcus spermaticus is straight, unforked, and

laterally placed. The distal end of the hemipenis is shallowly forked and provided with fine spines which become enlarged proximally. Two millimeters from the base, on the medial side of the sulcus, is a moderately enlarged recurved spine with a slightly smaller spine beside it.

Dentition.—Maxillary teeth about fifteen, slender and gently recurved, subequal in length, except the last two, which are reduced to about one-half the length of the others. Mandibular teeth fifteen, largest anteriorly, and gradually reduced posteriorly.

Size.—The largest male of this species examined was 320 mm. in total length (fifteen specimens), the largest female 412 mm. (thirty-one specimens). A summary of the average total length and the tail/total length ratio is given in Table 9. These snakes appear to be more slender in proportion to body length than *S. dekayi* or *S. occipito-maculata.*

VARIATION

Scutellation.—Variation in scutellation is summarized in Table 9. The population has been arbitrarily treated in two sections, the one north of a line through Florida at the latitude of Orlando, the other south. It is evident that there is an increase in numbers of both ventrals and subcaudals to the south. The sum of the ventrals and subcaudals averages 190.9 in the north and 203.1 in the south. It is usually possible to tell whether a given specimen is from northern or southern Florida on the basis of ventral and subcaudal counts alone. The amount of sexual dimorphism in numbers of ventrals and subcaudals is apparent on consulting Table 9. Variation in numbers of the various plates of the head is shown in Table 10. The supralabials are always seven, the anterior temporal always single. The dorsal scales are uniformly in fifteen rows. There is no evidence of intergradation of this species with *S. dekayi.*

TABLE 9.—Summary of Regional Variation in Certain Characters of *Storeria victa* Hay.

	Males			Females		
	No.	Extremes	Average	No.	Extremes	Average
Ventrals						
North	12	131-140	134.4	22	130-148	139.8
South	4	134-142	138.9	11	140-148	143.6
Subcaudals						
North	10	52-62	57.5	22	46-56	51.2
South	4	65-69	66.7	10	48-64	59.5
Ventrals — Subcaudals						
North	10	73-80	77.0	22	77-96	88.1
South	4	65-75	72.0	10	79-92	84.1
Total Length						
North	11	296	252.0	22	412	287.4
South	4	320	259.8	9	402	332.0
Tail/Total Length Ratio						
North	10	21.4-25.6	23.9	17	18.0-23.2	20.7
South	4	25.6-28.9	26.9	10	18.0-25.2	22.2

TABLE 10.—Summary of Variation in Head Plates in 48 Specimens of *Storeria victa* Hay.

Infralabials			6/6	7/7	8-R	8-L	8/8
Frequency in per cent			2.1	normal	2.1	8.3	2.1
Preoculars				1/1	2-R	2-L	2/2
Frequency in per cent				normal	8.3	2.1	4.2
Postoculars			1-L	2/2	3-L	3/3	
Frequency in per cent			2.1	normal	6.2	2.1	
Posterior Temporals	1-R	1-L	1/1	2/2	3-R	3-L	3/3
Frequency in per cent	6.2	6.2	6.2	normal	8.3	6.2	8.3

Coloration.—There is much variation in the intensity of the markings on the head and belly. The light band across the rear of the head may be white, or hardly lighter than the dorsal ground color. The dark occipital marks may be black, or lightened to a point where they are hardly darker than the ground color of the body. The dark markings on the side of the head are relatively dull and obscure in specimens from southern Florida, while they are prominent in those from northern Florida. The light band on the occiput in adults of this species is similar to the juvenile coloration of *S. dekayi*. Occasional specimens from northern Florida have the head markings relatively obscure, while ones from as far south as Sarasota may have prominent head markings.

The dark mark on the side of the head typically covers the third to fifth supralabials and the adjoining portions of the lower labials; it may be confined to the fourth supralabial and involve only the adjoining margins of the third and fiifth. The lower labials are sometimes completely unmarked.

The anterior temporal frequently bears a dark horizontal stripe on the upper half of the scale, but sometimes only on the anterior margin.

Variation in the intensity of the spots on the sixth scale row is almost as great as in *S. dekayi*.

There is a tendency for each ventral to be provided with a single prominent spot a short distance from its lateral edge, as noted in the description of the type. These spots are often mixed with the smaller spots, and are frequently indiscriminately scattered over the belly; the spots tend to be elongate, and arranged in rows.

HABITAT

This species appears to inhabit moister localities than any other *Storeria*. Carr (1940) records it from near ponds, sloughs, and marshes, under logs and among floating water hyacinths. It is found under logs along the canals in the Everglades but the best known locality is Payne's Prairie south of Gainesville, where it has been taken among the water hyacinths, and under debris along the margin of the Prairie.

DISTRIBUTION

This species is known from the entire length of the Florida peninsula, north to southeastern Georgia. There are no records from the panhandle of Florida. The northernmost station known is the Okefinokee Swamp in Georgia.

AFFINITIES

The derivation of *Storeria victa* is not clear. In number of scale rows, it agrees with *S. occipito-maculata;* in other characters, i.e., the number of preoculars, the number of supralabials, and the general coloration, it seems more closely allied to *S. dekayi*. In its high number of ventrals and subcaudals it is more closely approached by *S. dekayi* than by *S. occipito-maculata* in this region (compare Tables). These characters seems to indicate *S. dekayi* to be the most closely relater form. A point against this interpretation lies in the fact that *S. dekayi* is probably derived from *S. storerioides* (or a *storerioides* ancestor) which has fifteen scale rows. I am reluctant to assume that in the course of evolution the scale rows would be increased and subsequently again reduced. On the evidence available, however, *S. dekayi* must be accepted as the form from which *S. victa* has evolved.

The order of difference between this species and other species of *Storeria* is much greater than that distinguishing *S. occipito-maculata obscura,* the other endemic form of the Floridian region. *Storeria victa* is probably a form that evolved during the insulation of a portion of Florida, and from a population of *S. dekayi* thus isolated.

The reunion of the Floridian island with the mainland must have occurred after a period of isolation sufficiently long for the development of intersterility so that interbreeding with *S. dekayi* was no longer possible. *S. victa* continues its specific integrity, though the northern limit of its range now overlaps that of *S. dekayi*.

LOCALITY RECORDS

Specimens examined as follows:

FLORIDA: *Alachua County*—UMMZ 65318, 79578; Coclough's Hill, UFC 1655; Gainesville, CORNELL 1939, FMNH 8560, OUMZ R-294, UFC 703; Payne's Prairie, south of Gainesville, AMNH 50490, CM 20115, CORNELL 1736, ERA Cape Sable, CM 20076; Royal Palm Park, CORNELL 1690; eight miles north of (six specimens), UFC—, 80, 1858, URMNH 6720. *Dade County*—CORNELL 3518; Cape Sable, CM 20076; Royal Palm Park, CORNELL 1690; eight miles north of Homestead, ZSP 506; Miami, UFC 286, CM 19834; Paradise Key, MCZ 12752, 13886, CAS 54668. *Duval County*—Jacksonville, MCZ 15718. *Indian River County*—Sebastian, MCZ 13952, 16199, 16200, 38578, 56990. *Lake County*—Leesburg, CM 19858. *Madison County*—Indian Reservation, Lee City, AMNH 21239. *Sarasota County*—Sarasota, FNB—. *Seminole County*—Sanford, CM 386. "North Florida," ERA 45A; "Seven Oaks," AMNH 2335.

GEORGIA: *Charleston County*—Okefinokee Swamp, Billy's Island, CORNELL 6237, 6239.

Introduction to Storeria dekayi

Pattern characters useful in working out the races of *Storeria dekayi* are found in the arrangement of the dark spots along the back, on either side of the middorsal line. These may be minute flecks or prominent spots, as much of the black pigment composing the spots is not on the scales themselves, but on the skin between the scales. Thus females that have the body distended with developing embryos during the early summer will have the scales spread, more of the skin between the scales showing, and in consequence have more

prominent dorsal spots. This is not always the explanation of the variation in the intensity of the spots — there actually is a graded series from those with less dark pigment, to those with more. There is, however, no geographic correlation in the intensity of dorsal marks. In certain specimens the marks of each side, whether light flecks or heavy spots, do not form discrete pairs, but fuse medially to form short mid-dorsal transverse bars. The marks about one-third of the way back on the body are the first to fuse, and individual specimens are found with the anterior dorsal spots in separate pairs, those behind fused to form crossbars and those toward the rear of the body again separate. Specimens from the Mississippi Valley, particularly the lower and eastern parts of this vast area, and those from the southern portion of the Atlantic coastal plain in the United States, show the fused condition of the dorsal spots. In New England, and in the northeast generally, as well as along the northern Atlantic coastal plain, the spots are separate. They are also separate in the snakes from Honduras through Guatemala and Mexico, into Texas, Oklahoma, Kansas, and to the north, as well as east along the Gulf coastal strip to Louisiana. Thus we find the separate condition in the east and northeast separated from the similar condition to the west and south, by the crossbar condition in the Mississippi Valley.

The markings of the head of *Storeria dekayi* also vary geographically. Over all of the eastern United States, the anterior temporal scale is marked through its center or rear with a vertical or oblique dark bar. Specimens from eastern localities may occasionally have this bar interrupted. In the west, from Texas to Iowa, the temporal lacks the bar, and is either completely unmarked, or with a little dark pigment along one of its margins. Occasional specimens are found as far east as Illinois or Indiana with the temporal unmarked. Along the eastern Mexican coastal plain snakes are found in which the temporal scale bears a horizontal dark stripe. This usually obscures the upper half of the scale, but it is sometimes darkest along the middle of the scale and lighter above. The transition from this condition to that of the unmarked temporal is seen in specimens from the Texas coastal strip, although occasional specimens from as far east as Louisiana, and one from western Florida show a horizontal stripe. To the south as far as Puebla, there is a well developed stripe in all specimens seen. Snakes from south of the Isthmus of Tehuantepec have the stripe faint and incomplete posteriorly.

The supralabials in this species are marked to a varying degree. The pigment is usually accumulated along the sutures between the scales and forms wedge-shaped marks broad above and narrow below. The most prominent of these are the one below the orbit on the fourth supralabial, and that on the suture between the last two supralabials. The mark below the eye is best developed in snakes from the interior of Texas and from Oklahoma. In these it obscures almost all of the fourth supralabial, sometimes leaving a narrow light area along the labial margin. To the north and northeast this mark becomes reduced to a dark wedge with its apex at the point where the fourth and fifth supralabials meet the labial margin, and with its base along the upper margin of the scale bordering the orbit. To the south, along the Mexican coastal strip, it is absent or persists as a faint dusting of pigment in the

upper rear corner of the scale. The mark across the suture between the last two supralabials is a continuation of the vertical temporal stripe of specimens from the east, persisting in western snakes though the temporal mark is absent. In the snakes from the Mexican coastal strip and south, it is completely absent as are all labial marks.

The dark paired marks on the occiput also vary. In the Texas region they are elongate, sometimes as long as broad. To the north and northeast they become narrower, and in the northeastern states are reduced to narrow crescents. South of Texas they are reduced until they are hardly larger than the paired dorsal spots that follow them on the back.

Juvenile specimens of all the races of *Storeria dekayi* have distinctive head coloration as follows. There is a whitish area on the side of the head in the region of the forward portion of the anterior temporal and the fifth supralabial. There is another strong white patch of larger size behind this involving the posterior temporals, and the row of scales immediately behind these. This patch is continuous with the white of the venter. Dorsally the white extends as a narrow band across the back just behind the parietals and just anterior to the dark occipital markings. The white band is here about one scale in width. The light condition of the rear of the head, anterior to the paired dark markings of the occiput is pronounced in all young and persists until the snakes have reached a length of 135 to 145 mm. Some specimens of 150 mm. have the lightening of the rear of the head almost as pronounced as the newly-born young, but mostly between 150 and 160 mm. there is a decided dimming of the white. Snakes as large as 200 or 225 mm. will sometimes have the rear of the head slightly lighter than the remainder of the body, but beyond this size the adult coloration is reached.

The number of ventrals and of subcaudals show similar clinal trends — low in the northeast, increasing to the south. As the ventrals are high in the females and low in the males, and the subcaudals low in the females and high in the males, summation of the ventrals plus subcaudals roughly balances the differences between the sexes and the figure which represents the sum of the ventrals and subcaudals is about the same for both sexes in any one region; it thus lends itself to the examination of clinal variation in these characters.

The chin shields in this species are in two pairs, usually subequal in length, with the exception of the form from the vicinity of Mt. Orizaba in Mexico, in which they are in three pairs.

The combinations of characters in any one area are striking, and by close attention to them it is possible to determine the region from which any individual snake has come. The transitions from one to the other do not always coincide geographically, so that much consideration has been necessary to determine which of two characters shall be the decisive one in delimiting two subspecies, and further how the characterization of each race should be stated to most closely approximate the natural subspecies with the smallest areas of intergradation.

STORERIA DEKAYI DEKAYI (Holbrook)
Dekay's Brown Snake

Figs. 26-37

Tropidonotus dekayi Holbrook, N. Amer. Herp., vol. 4, p. 53 (partim), 1842; Dekay, New York Fauna, Rept., p. 46 (partim), 1842.

Tropidonotus occipito-maculatus Holbrook. N. Amer. Herp., vol. 4, p. 55 (partim), 1842.

Ischnognathus dekayi Duméril and Bibron, Erp. Gen., vol. 8, pt. 1, p. 507, 1854; Boulenger, Cat. Snakes Brit. Mus., vol. 1, p. 286 (partim), 1893.

Storeria dekayi Baird and Girard, Cat. N. Amer. Rept., pt. 1, Serpents, p. 135 (partim), 1853; Cope, Rept. U. S. Nat. Mus., p. 1000 (partim), 1900; Stejneger and Barbour, Check List N. Amer. Amph. Rept., ed. 4, p. 131 (partim), 1939.

The description of *Tropidonotus dekayi* was based on specimens from Massachusetts, New York, Michigan, and Louisiana. Apparently only one of the types is now in existence, a female, number 5832, in the collection of the Academy of Natural Sciences of Philadelphia. This individual, from the Holbrook collection at the Academy bears the locality data, "Massachusetts" (see Figs. 32-37).

The ventral and subcaudal counts are given by Holbrook for only one specimen, total 185, indicating a specimen from the south. The specimen he illustrates (Pl. 14) shows the characters of what is here designated as subspecies *texana*, i.e., with separate dorsal spots and a clear temporal. But the description of the coloration is too general to be linked with any of the races recognized here. Furthermore, it is evident from the widespread localities given for the cotypes, that the description is a composite. I choose the first mentioned locality, Massachusetts, as the type locality, and select ANS 5832 as the lectotype. This choice makes for the least disturbance of the nomenclature.

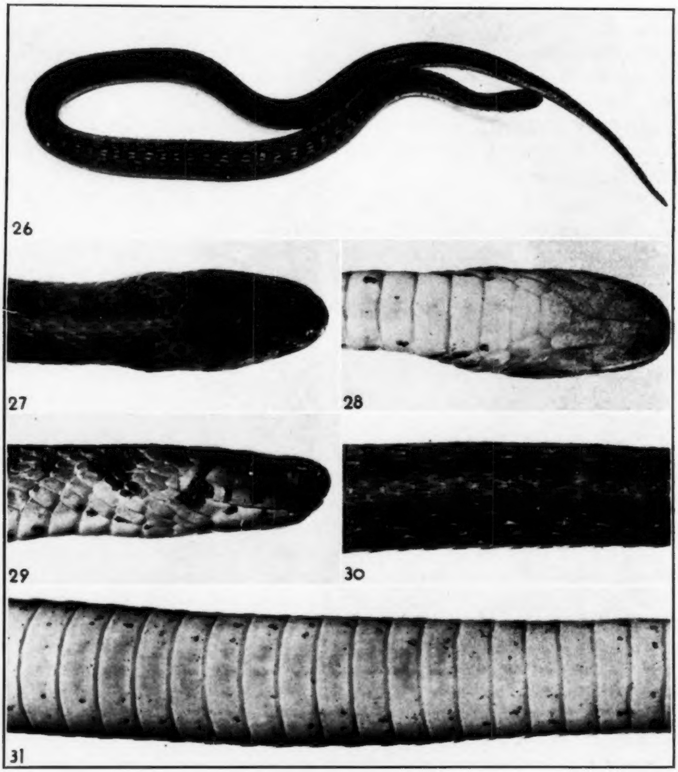
The lectotype is in good condition. The head plates are normal with the exception of the right upper postocular, which is fused with the supraocular. The preoculars are one on each side, the left postoculars two, the temporals 1-3 on each side. The chin shields are in two pairs, subequal in length, the anterior somewhat damaged. Both supralabials and infralabials are seven on each side. The body scales are all keeled, posteriorly emarginate, and in seventeen rows. There are 129 ventrals, and 44 paired subcaudals, thus within the range of numbers in subspecies *dekayi*. The total length is 382 mm., of which the tail comprises 20.0 per cent.

The top of the head is heavily peppered with black excepting the outer margins of the parietals. The upper half of the fourth supralabial is marked with black as are the areas about the sutures between the third and fourth, the fourth and fifth, and the sixth and seventh supralabials. The latter mark is continued below to darken the suture between the sixth and seventh infralabials, and above to darken more than half of the width of the rear portion of the anterior temporal. In this the specimen is somewhat abnormal, as a complete vertical bar across the temporal proves to be characteristic of this race. The occipital marks are crescentic and separate on the middorsal line.

The dorsal spots on the sixth and seventh scale rows of the body are pronounced. There are weak lateral rows of spots alternating with the dorsal spots. The belly is laterally flecked with black, particularly on the anterior portion of the body. There are no flecks evident on the tail, or on the posterior portion of the body.

DESCRIPTION

Diagnosis.—The subspecies *dekayi* is characterized by the low number of ventrals and subcaudals (their sum equalling 175 or less in 94 per cent of specimens examined), by the discrete paired spots along the back, and by the vertical or diagonal dark bar across the rear of the anterior temporal.



Figs. 26-31.—*Storeria dekayi dekayi*. All figures of specimen from near Auburn, New York, photographed in life. Fig. 26. Dorso-lateral view of entire snake, slightly reduced. Fig. 27. Dorsal view of head, slightly enlarged. Fig. 28. Ventral view of head, slightly enlarged. Fig. 29. Lateral view of head, slightly enlarged. Fig. 30. Dorsal view of body, slightly enlarged. Fig. 31. Ventral view of body, slightly enlarged.

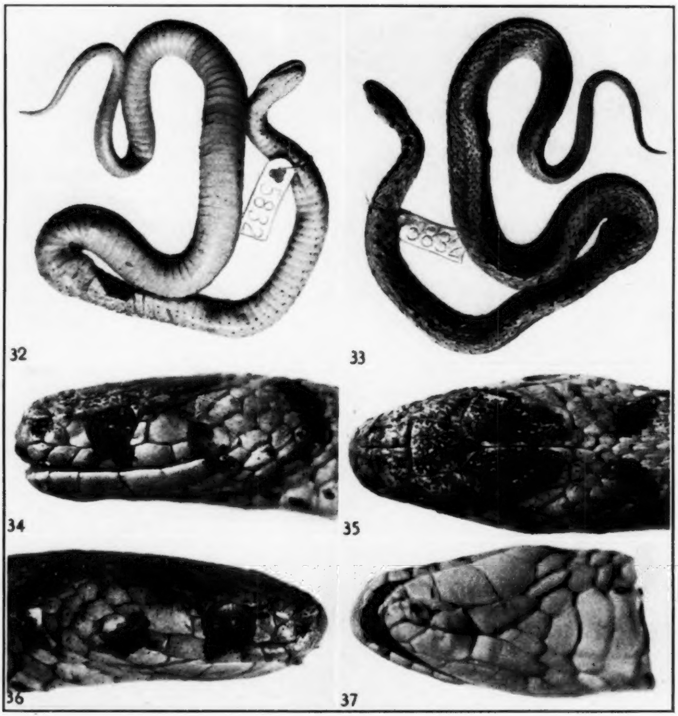
Scutellation.—Dorsal head plates normal for the genus; anterior nasal slightly smaller than posterior, higher than long, frequently fused with the latter, particularly above the nostril; posterior nasal approximately equilateral; preocular entire, half again as high as broad; supraocular twice as long as wide; postoculars normally two, the upper usually slightly larger; temporals normally 1-2, the anterior larger than the two posterior combined; upper labials normally seven, the third and fourth entering the orbit, the seventh largest; lower labials normally seven, the fourth and fifth each not less than twice the area of the others, first pair in contact between the mental and the anterior chin shields; mental triangular, broader than long; chin shields in two pairs, the anterior pair in contact throughout their length along the median line; posterior chin shields normally approximately equal in length to the anterior chin shields, but slightly narrower, truncate anteriorly, gently tapering to a rounded apex posteriorly, normally in contact for the anterior third of their length, divergent and separated posteriorly by small scales; body scales in seventeen rows, all keeled, emarginate posteriorly, first row broadest, apical pits not apparent.

Ventrals 112 to 125 in males (one hundred and forty-six specimens), 119 to 134 in females (one hundred and seventy-seven specimens); anal divided; subcaudals divided, in males in 43 to 57 pairs (one hundred and thirty-nine specimens), in females in 36 to 49 pairs (one hundred and seventy-three specimens).

Coloration.—This species is brown or sometimes grayish in general appearance. The head is normally peppered with dark brown or black. From the dark dorsum of the head there is a vertical or oblique stripe extending ventrally across the rear of the temporal, and the region adjoining the suture between the sixth and seventh infralabials. The mark across the anterior temporal is characteristic of this subspecies, sometimes obscuring the entire rear half of the temporal. The markings of the supralabials are variable, but there is usually some dark pigment at the rear of each labial except the seventh. Most constant is the mark on the fourth labial, below the orbit. This mark is usually wedge-shaped, broadest dorsally. The infralabials are often clear and unmarked, but frequently with some flecks adjoining the sutures between the scales. The chin shields and mental are usually clear whitish. On the occiput there is a pair of dark crescentic marks two scales in width. These are most often separate on the median dorsal line, and extend laterally to the ventrals or a scale or two above.

The markings on the body are exceedingly variable. With the skin stretched it is apparent that there is a fundamental checkered pattern similar to that found in the garter snakes (*Thamnophis*), dark markings being more evident on skin between the scales, and along the margins of the scales than on the scales themselves. On the sixth and seventh rows of scales there is a series of squarish dark marks, usually alternating with similar but smaller ones below on the third and fourth scale rows. There are often darkened areas bordering the scales of the first row, alternating with the second series of

marks. Except for these dark areas, the skin between the scales is whitish or yellowish. The dark markings may be prominent, or scarcely apparent. It is characteristic of this subspecies that the dark markings of the sixth and seventh scale rows are not fused across the back to form short crossbars as in the subspecies *wrightorum*, though occasional specimens may have a few such spots. The middorsal three scale rows are frequently uniform with the remainder of the dorsum; they may be lighter in color to form a light dorsal stripe, bordered by the uppermost of the series of spots described above. This stripe varies from a light clay color to a shade of brown or gray only faintly distinguishable from the ground color. The dorsal spots become smaller posteriorly so that they cannot be made out on the tail and are frequently obscure on



Figs. 32-37.—*Storeria dekayi dekayi*. All figures of Lectotype, ANS 5832, from "Massachusetts," Fig. 32. Ventral view of whole specimen, slightly reduced. Fig. 33. Dorsal view of whole specimen, slightly reduced. Fig. 34. Lateral view of head and neck several times life size. Fig. 35. Dorsal view of head and neck, several times life size. Fig. 36. Lateral view of head and neck, several times life size. Fig. 37. Ventral view of head and neck, several times life size.

the rear of the body. The number of spots in that portion of the body included in the first fifty ventrals varies from eighteen to twenty-nine.

The venter is clear and whitish, often washed with pale pink or brownish. It is usually flecked with black laterally. These flecks are more pronounced anteriorly and become fewer posteriorly, often being completely absent on the rear of the body and tail. The lateral edges of the ventrals are often a little darkened by invasion of some of the dorsal ground color.

Hemipenis.—The retractor penis muscle inserts at the level of the twentieth to the twenty-fifth subcaudal. The hemipenis itself reaches the region of the eighth subcaudal. Tht organ is finely spinose distally, the spines becoming gradually larger proximally, and culminating in one much enlarged spine on the median side of the base of the sulcus. There are two or three lesser but enlarged spines just distad of this enlarged spine. The sulcus spermaticus is straight. The hemipenis is not expanded distally as in *S. occipito-maculata.*

Dentition.—The maxillary teeth are fifteen in number, slender, and gently recurved. They are subequal in length, except the last several which are very slightly reduced. The dentary is provided with sixteen to eighteen teeth, largest anteriorly and decreasing gradually posteriorly.

Size.—The largest male of this species measured was 324 mm. in total length, the largest female 436 mm. A summary showing geographic variation in maximum size and average length of adults as well as the tail/total length ratio is given in Table 11.

VARIATION

Scutellation.—The data on the numbers of ventrals and subcaudals are summarized in Table 11. The ventrals are higher in females and lower in males, and the subcaudals higher in males and lower in females, though with some overlap of the extremes. Geographic variation in numbers of ventrals and subcaudals is not pronounced in this race. The largest series from a single state, all subspecies *dekayi,* is from New York; 26 males and 36 females have ventrals 117-125, average 121.6 and 123-132, average 127.4; subcaudals in 24 males and 29 females are 46-54, average 49.5, and 36-48, average 42.5.

The variation in number of head plates is shown in Table 12. The variation in number of infralabials is much greater than that of the supralabials and the number of postoculars is more variable than the number of preoculars. The normal two posterior temporals may be reduced by fusion to one, or may be increased to five.

A single male specimen from Mt. Washington, Berkshire County, Massachusetts, OUMZ R-484-11, has more than seventeen scale rows. Its scale formula is 17-18-19-20-19-17. A single female specimen from Ferry Landing, Virginia, USNM 8951, has the anal plate entire.

Coloration.—The amount of pigmentation on the labials varies greatly. The top of the head is sometimes almost completely black and it may be rarely almost a clear brown. The vertical temporal bar characteristic of this

TABLE 11.—Summary of Regional Variation in Certain Characters of *Storeria dekayi dekayi*.

	Northeast			Eastern Upland			North Central			Atlantic Coastal Plain		
	No.	Extremes	Av.	No.	Extremes	Av.	No.	Extremes	Av.	No.	Extremes	Av.
Ventrals												
Males	31	115-125	121.0	49	116-125	120.6	17	115-125	121.2	49	112-125	118.8
Females	39	124-130	126.3	62	123-132	126.6	34	124-134	127.5	42	120-132	125.4
Subcaudals												
Males	30	47-55	50.2	46	46-55	49.9	16	48-55	51.3	47	43-57	50.8
Females	38	37-49	42.9	60	36-48	42.6	34	40-49	45.2	43	38-48	43.7
Ventral + Subcaudals												
Sexes combined	70	163-178	170.2	106	161-178	170.0	50	164-175	172.6	89	158-177	169.2
Ventrals — Subcaudals												
Males	30	64-76	70.7	46	64-77	70.8	17	65-75	69.7	47	55-75	68.0
Females	39	75-90	83.2	60	75-91	83.9	33	77-94	82.7	42	75-89	82.0
Total Length												
Males	26	331	266.9	39	336	262.6	14	306	252.6	34	324	250.4
Females	33	392	300.2	49	436	296.4	29	409	314.6	29	368	284.2
Tail/Total Length Ratio												
Males	31	21.2-31.6	23.4	45	20.0-26.3	23.6	18	20.0-25.5	23.6	47	19.1-26.9	24.0
Females	39	16.7-23.0	19.6	60	17.4-22.2	19.5	32	18.4-22.5	20.1	39	17.9-22.6	20.4

For "Extremes" under "Total Length" only the maxima are given. The average total length is derived from specimens over 175 mm. in length. (These are assumed to be mature.) Regions used may be outlined as follows: Northeast — Quebec and New England; Eastern Upland — New York, Pennsylvania, West Virginia, Kentucky, Tennessee; North Central — Ohio, Ontario, Michigan; Atlantic Coastal Plain — New Jersey to South Carolina.

subspecies is rarely interrupted. The dorsal spots may be prominent or almost entirely wanting. The flecking of the belly may be very prominent, almost as in *S. victa,* or the flecks of pigment may be almost totally lacking. An albino specimen from Washington, D. C., is white, with a very faint indication of the dorsal body spots.

HABITAT

In my experience this is a snake of relatively dry, well-drained situations where it secretes itself under flat stones. In eastern cities it is often abundant in vacant lots where it may be found under bits of trash as tarpaper, tin, cardboard, boards, or under stones. This is somewhat at variance with DeKay's statement (1842) that all specimens he had seen were either in or near water. DeKay reports that the specimen he figures was taken swimming across a large saltwater bay on the northern shore of Long Island. At Flushing, Long Island, these snakes are abundant along hillsides and embankments above a freshwater marsh, but absent from an adjoining saltwater marsh.

TABLE 12.—Summary of Variation in Head Plates in 323 Specimens of *Storeria dekayi dekayi.*

Supralabials				6–R	6–L	7/7	8–R	8–L			
Frequency in per cent				1.9	0.9	normal	1.2	1.2			
Infralabials	5–R	5/5	6/6	6–R	6–L	7/7	8–R	8–L	9–R	9–L	
Frequency in per cent	0.3	0.3	0.3	2.0	3.1	normal	3.7	4.0	0.6	0.3	
Preoculars						1/1	2/2				
Frequency in per cent						normal	0.3				
Postoculars			1/1	1–R	1–L	2/2	3–R	3–L	3/3		
Frequency in per cent			0.9	2.5	2.2	normal	5.3	5.9	2.8		
Posterior Temporals			1/1	1–R	1–L	2/2	3–R	3–L	3/3	4–L	5–L
Frequency in per cent			13.0	8.0	9.3	normal	7.7	5.3	6.9	0.3	0.3

The evolutionary success of *Storeria dekayi dekayi* is attested by its survival even within the limits of such large eastern cities as Boston, New York, Philadelphia, and Washington. Individuals are rarely seen on the surface except perhaps at dusk when they seem most actively on the prowl for food. That the successful survival of this form in the urban situation is not alone due to their secretive habits is evident from the fact that similarly secretive snakes like *Diadophis punctatus, Carphophis amoena, Tantilla coronata* and *Storeria occipito-maculata,* have not survived in such areas.

DISTRIBUTION

The typical race of *Storeria dekayi* occurs from southern Quebec through New England and New York to western South Carolina and eastern Tennessee in the uplands. It intergrades to the south and west with *S. dekayi wrightorum.* Intergrading specimens are found along the Atlantic coastal plain from Virginia south to South Carolina, around the southern end of the Applachians and north along the western border of the interior low plateau to Illinois and Ontario.

LOCALITY RECORDS

Specimens examined as follows:

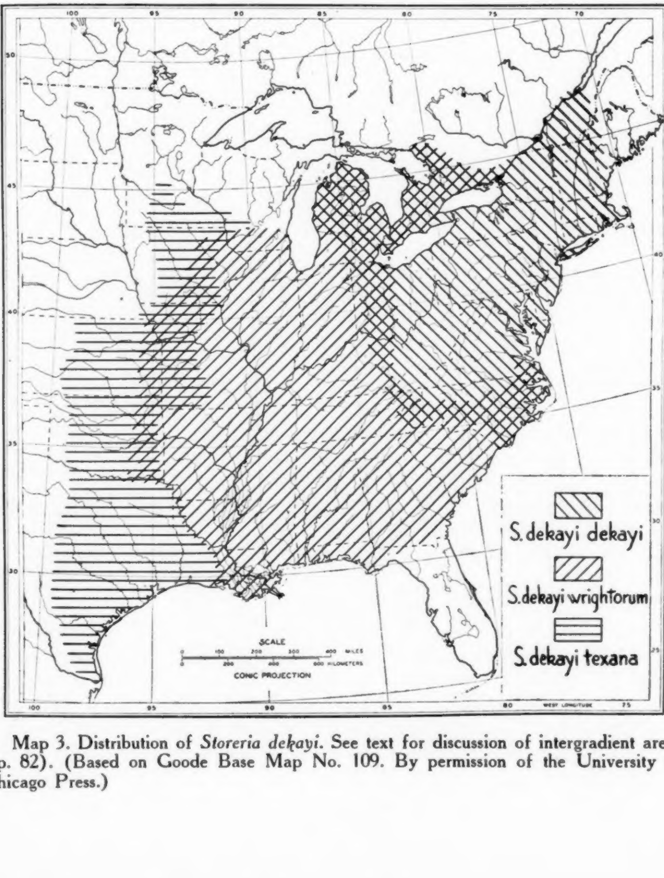
CANADA

ONTARIO: *Essex County*—Point Pelee, ROMZ 87. *Kent County*—Rondeau Park, ROMZ 2048. *Middlesex County*—Kerrwood, ROMZ 170. *Norfolk County*—Lake Erie, Turkey Point, CM 21021; Long Point ROMZ 1997-98, 1994, 2000, 2046, 2051. *Parry Sound County*—Parry Sound, ROMZ 2094; Point Au Baril, CM 6357. *Prince Edward County*—Garrett's Island, ROMZ 2433. *Waterloo County*—near Rockton, ROMZ 2803. *Wentworth County*—Aldershot, CNM 1099; Hamilton CNM 1078, 1178, 1314. *York County*—Toronto (Don Valley), CNM 108, USNM 25343; Humber River, Toronto, ROMZ 3708.

QUEBEC: *Jacques Cartier County*—Montreal, CORNELL 3429. *Portneuf County*—St. Catherine's, USNM 4986.

UNITED STATES

CONNECTICUT: *Fairfield County*—Saugatuck, AMNH 7707. *Hartford County*—three miles west of Hartford, CM 12526.



Map 3. Distribution of *Storeria dekayi*. See text for discussion of intergradient areas (p. 82). (Based on Goode Base Map No. 109. By permission of the University of Chicago Press.)

DELAWARE: *New Castle County*—two miles south of Newark, ZSP 669.

DISTRICT OF COLUMBIA: Washington, USNM 1949, 4900, 17282-86, 17447-54, 17563-64, 44160, 44924, 44337, 80316, 37505, 75117, 17288, 67456, 66998-67000, 5891.

KENTUCKY: *McCreary County*—Cumberland Falls, CA 7442. *Rowan County*—Morehead, RB—.

MAINE: *Cumberland County*—Westbrook, USNM 17834. *Oxford County*—Upton, MCZ 2390. *York County*—York Harbor, FMNH 33752.

MARYLAND: *Baltimore County*—Baltimore, USNM 27466, 27492-94, 29352-53. *Dorchester County*—Cambridge, MCZ 29781; two miles southeast of Golden Hill, ZSP 2121-22. *Montgomery County*—near Glen Echo, USNM 53391; Cabin John, USNM 54326; Plummer's Island, USNM 65147. *Prince George County*—Berwyn, USNM 36867.

MASSACHUSETTS: *Berkshire County*—Mt. Washington, OUMZ R478, R484, R484-1-3, R484-5, R484-11, R484-15. *Dukes County*—Cuttyhunk, Elizabeth Ids., AMNH 6411, 6415-16. *Essex County*—Wenham, MCZ 737. *Franklin County*—Warwick, MCZ 2366. *Hampden County*—Chicopee, MCZ 733; Springfield, MCZ 2258, 2291. *Hampshire County*—Northampton, ANS 12304, 12310. *Middlesex County*—Arlington, UMMZ 65951; Newton Center, MCZ 18976; Sherborn MCZ 726, 2385; Cambridge, MCZ 166-67, 738, 2329, 2343, 2470, 4484; Waltham, MCZ 375; Framingham, USNM 1960; Feltonville, Hudson, MCZ 2376; Woburn MCZ 729. *Suffolk County*—Brookline, MCZ 730; West Roxbury, MCZ 2492. *Worcester County*—Berlin, MCZ 732; near Auburn, USNM 1944. "Massachusetts," ANS 5832, USNM 55920, UMMZ 71412.

MICHIGAN: *Benzie County*—Crystal Lake, UMMZ 70509. *Calhoun County*—Battle Creek, UMMZ 79132. *Crawford County*—Near Lovells, UMMZ 76180. *Huron County*—Caseville, UMMZ 37952; Sand Point, UMMZ 37731. *Jackson County*—Crass Lake Twp., FNB—; three miles north Jackson UMMZ 65288. *Manistree County*—East Lake, UMMZ 46024-26. *Mason County*—Bass Lake, UMMZ 56745. *Mecosta County*—UMMZ 63385. *Muskegon County*—North Muskegon, UMMZ 78531. *Oakland County*—Pontiac, UMMZ 35864. *Roscommon County*—UMMZ 47448. *Shiawassee County*—UMMZ 74548. *Washenau County*—Ann Arbor, FNB—, UMMZ 32778, AMNH 37359; Ypsilanti, UMMZ 32499. *Wayne County*—Grosse Is., UMMZ 42496.

NEW HAMPSHIRE: *Cheshire County*—Dublin, USNM 24128; Fitzwilliam, USNM 52428; one mile southwest Rindge, UMMZ 86336. *Hillsboro County*—Amherst, MCZ 725; Peterborough FNB—. *Merrimack County*—UMMZ 84639. *Rockingham County*—Northampton, MCZ 5598. *Sullivan County*—UMMZ 86337.

NEW JERSEY: *Atlantic County*—two and one-half miles north of Weymouth, CFK 111. *Bergen County*—Fort Lee, AMNH 3386, 31852; *Rutherford*, AMNH 24692-93. *Camden County*—Camden, ZSP 208. *Cumberland County*—Vineland, CFK 84, 121, USNM 66658-59. *Essex County*—Newark, CORNELL 1869; Caldwell, AMNH 3375. *Hudson County*—Secaucus, AMNH 7543-46. *Monmouth County*—Allaire, UMMZ 74463, 77143; Long Beach UMMZ 76576; Spring Lake, USNM 100828. *Morris County*—Near Dover, CM 6194; Newfoundland, AMNH 43903. *Ocean County*—Lakewood, CORNELL 1989; East Lakewood, CORNELL 1275. *Somerset County*—Watchung, AMNH 43890, 43946. *Union County*—Plainfield, AMNH 43932, 43958. "New Jersey," AMNH 6713, 6710-11, UMMZ 77141.

NEW YORK: *Albany County*—near Rafts Pond, URMNH 3590. *Bronx County*—New York City, AMNH 61794, 61797-99, 61801, MCZ 6861, OUMZ R-486. *Cattaraugus County*—Olean, AMNH 60203. *Chautauqua County*—Clymer, URMNH 4138. *Chemung County*—Van Etten, CORNELL 1873. *Cortland County*—south end Skaneateles, Grout Brook, CORNELL 2614. *Kings County*—Bergen Beach, AMNH 4174-75, 2378-79, 2090-92, LMK 33453. *Monroe County*—University of Rochester River Campus, URMNH 2144, Rochester URMNH 3594, 3139-41; North Greece, URMNH 3428. *Nassau County*—Glen Cove City, Long Island, AMNH 28371;

Freeport, Long Island, URMNH 2548-49. *New York County*—New York City, AMNH 3379, 9612, 24736, 61800, 61784-86, 61792-93, 61795-96. *Onondaga County*—Near Campus Syracuse University, FNB—. *Ontario County*—Near Honeoye Lake, SUMNH. *Orange County*—Goshen, URMNH 1448. *Putnam County*—Cold Spring, ANS 20875. *Queens County*—OUMZ R-145, R-68-69; Flushing, CORNELL 1095, AMNH 24951, 59708-11, 59714-19, 59721; Lynbrook, AMNH 19446; Jamaica, AMNH 4150; Elmhurst, Long Island, AMNH 22418. *Rensselaer County*—Berlin, USNM 82551. *Richmond County*—Staten Island, OUMZ R65, CORNELL 2478. *Rockland County*—AMNH 3382; Palisades Interstate Park, CORNELL 1452. *Saratoga County*—Fortsville, URMNH 2567. *Tompkins County*—Camp Barton, CORNELL 1372. *Warren County*—Lake George, USNM 80317. *Wayne County*—North Rose, USNM 49634. "Long Island," USNM 55427.

NORTH CAROLINA: *Brunswick County*—four miles south Supply, CM 17993. *Buncombe County*—Asheville, USNM 44177. *Cabarrus County*—Concord, AMNH 12590. *Craven County*—New Bern, MCZ 2489, USNM 6427. *Gates County*—Winton, AMNH 39847. *Harnett County*—Buies Creek, OUMZ R-433. *Hyde County*—Lake Landing, CM 15107. *New Hanover*—Wilmington, UFC 119; Cape Fear River, Wilmington, USNM 37058. *Wake County*—Raleigh, SUMNR 1725, CM 5583.

OHIO: *Ashtabula County*—five miles north of Geneva, CM 13084, 14033. *Erie County*—Sandusky, UMMZ 32784-85. *Franklin County*—near Columbus ROMZ 3761, USNM 1957. *Lucas County*—Toledo, UMMZ 75622. *Ottawa County*—CM 9485.

PENNSYLVANIA: *Allegheny County*—near Wilkinsburg, CM 19267. *Bedford County*—Bedford, MCZ 2411. *Bucks County*—Tinicum, ANS 20874. *Butler County*—near Slippery Rock, Wolf Creek, CORNELL 9060. *Dauphin County*—Harrisburg, MCZ 5908, CM 7591. *Delaware County*—Addingham ANS 21510; Clifton Heights, ANS 22025; Darby Creek above Addingham, ANS 22026; Tinicum, ANS 19062; Drexel Hill, ZSP 1321, 652, 528-30, 533-34. *Forest County*—twelve miles northeast of Tionesta, CM 9499. *Mercer County*—Greenville, CM 7750. *Montgomery County*—Camp Delmont, Sumneytown, ZSP 2305; Penn Lynne, ZSP 549-50. *Philadelphia County*—Torresdale, ANS 17676; West Philadelphia, ANS 21528; Philadelphia, UMMZ 46791, ANS 23001, 21479; Germantown, ANS 4011-13, 21953; Holmsburg, ANS 19047, 18344, 18347, 18592-93, 18670, 18710, 18941-42, 19040-41; in a quarry at Wingahocking Terrace, ANS 20919; Jones Neck, ANS 16625; League Island, ANS 15253-4. *Pike County*—AMNH 60668. *Somerset County*—three miles east of Stoystown, CM 10593. *Westmoreland County*—Mt. Lebanon, CM 19227.

RHODE ISLAND: *Newport County*—Newport, USNM 28651, 28666, 2874-84, 30051. *Washington County*—Narragansett Bay, USNM 28646-50. "Dutch Island," USNM 28667-8, 28652-65, 44172.

SOUTH CAROLINA: *Lexington County*—Batesburg, UMMZ 72241; Clemson, CLEM 207, 265. "South Carolina," AMNH 3387.

TENNESSEE: *Clairborne County*—Cumberland Gap, USNM 17966.

VERMONT: *Chittendon County*—Burlington, MCZ 2344. *Windham County*—West Wardsboro, AMNH 20411.

VIRGINIA: *Arlington County*—Arlington, USNM 25149. *Fairfax County*—Vienna, USNM 109701-3; Potomac Valley, one mile above Great Falls, UMMZ 36083; Little Hunting Creek, Mt. Vernon, UMMZ 63919. *Nansemond County*—Cypress Chapel, UMMZ 78201. *Norfolk County*—Dismal Swamp, Lake Drummond, USNM 44290. "Alexandria, Jackson City," USNM 24379-80; "Ferry Landing," USNM 8951; "Fort Humphries," LMK 108005-6; "Great Falls," AMNH 24972.

WEST VIRGINIA: *Mineral County*—Gerstell, CM 9575. *Preston County*—Snaggy Mountain, CM 15569. *Randolph County*—vicinity of Elkins, CM 6038, 6174-77, 9405, 9587, 12967, 12970-74, 12976, 20267, 15595, 15622, 15641, 15644-46, 15653-54, 15657, 15662, 15667-68, 15678, 15686, 15788-91, 15793. "West Virginia," CM 12977, 15665; "Elk River," USNM 33733.

Storeria dekayi wrightorum Trapido, subsp. nov.
Wrights' Brown Snake

Figs. 38-44

Tropidonotus dekayi Holbrook, N. Amer. Herpt., vol. 4, p. 53 (partim), 1842.

Ischnognathus dekayi Duméril and Bibron, Erp. Gén., vol. 8, pt. 1, p. 507 (partim), 1854; Boulenger, Cat. Snakes Brit. Mus., vol. 1, p. 286 (partim), 1893.

Storeria dekayi Baird and Girard, Cat. N. Amer. Rept., pt. 1, Serpents, p. 135 (partim), 1853; Cope, Rept. U. S. Nat. Mus., p. 1000-1003 (partim), 1900; Parker, Journ. Tenn. Acad. Sci., vol. 3, p. 85, 1939; Stejneger and Barbour, Check List N. Amer. Amph. Rept., ed. 4, p. 131 (partim), 1939.

No writer has seriously questioned the homogeneity of the population of *S. dekayi* inhabiting the United States up to the present time. The descriptions of this snake in the writings of eastern United States authors make no mention of the dorsal crossbars, and this has led to some question in the identification of specimens from the Mississippi Valley and the lower Atlantic coastal plain. The correlation of the cross-bar condition with a high number of ventrals and subcaudals in the same region provides a ready means of defining a population which seems worthy of nomenclatorial recognition.

DESCRIPTION

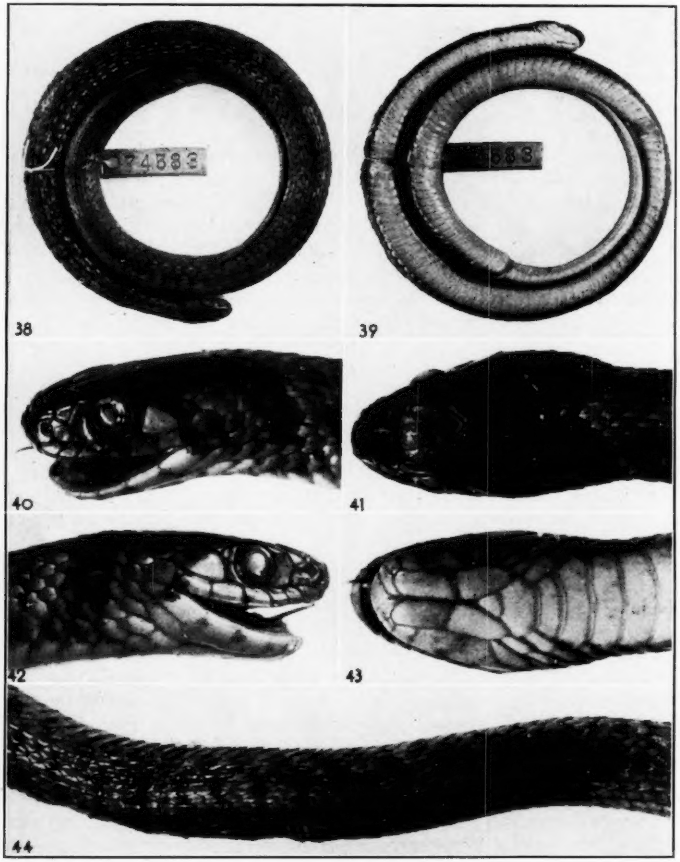
Holotype.—UMMZ 78583, adult female, taken at Reelfoot Lake, Tennessee, on April 9, 1933, by Norman Hartweg and Wesley Clanton.

Diagnosis.—*Storeria dekayi wrightorum* is similar to *S. d. dekayi* but differs in that the dorsal spots are fused to form short dorsal crossbands, and the sum of the ventrals and subcaudals is 176 or more (ninety-one per cent of specimens examined).

Scutellation of Holotype.—Dorsal head plates normal; nostril opening between anterior and posterior nasals, nasals separated by suture below and apparently above the nostril, sub-equal in size; preocular single, about twice as high as broad; postoculars two on the right, one on the left, upper and lower subequal; anterior temporal single, longer than high; posterior temporals two; supralabials seven on each side, the fourth and third entering the orbit, the first three labials somewhat smaller than the remaining four; infralabials seven on each side, in descending order of size, five, four, six, three, one, seven, two, the first pair in contact on the median line behind the mental; mental triangular; chin shields in two pairs, subequal, the anterior pair in contact on the median line, the posterior pair in contact anteriorly, but separated by small scales posteriorly; dorsal body scales in seventeen rows, all keeled, scale rows narrowest medially, becoming broader laterally, the first scale row the broadest; all scales except those of the first row emarginate posteriorly; apical pits not apparent; ventrals 136 and subcaudals 51.

Coloration of Holotype.—Head brownish, spotted with black anterior to the parietals, the parietals mostly black; sides of head brownish, with the upper half of the superior postocular black. A black vertical bar through the

rear half of the anterior temporal, this bar continuing ventrally across the suture between the sixth and seventh supralabials, and terminating on the posterior end of the sixth infralabial; wedge-shaped black mark on the posterior half of the fourth supralabial, with its apex on the labial margin and its base at the orbit; little black pigmentation on the rear upper corners of the



Figs. 38-44.—*Storeria dekayi wrightorum*. Figs. 38-43 of Holotype, UMMZ 74583, from Reelfoot Lake, Tennessee. Fig. 38. Dorsal view of whole specimen, slightly reduced. Fig. 39. Ventral view of whole specimen, slightly reduced. Fig. 40. Lateral view of head and neck, several times life size. Fig. 41. Dorsal view of head and neck several times enlarged. Fig. 42. Lateral view of head and neck several times enlarged. Fig. 43. Ventral view of head and neck several times enlarged. Fig. 44. Dorsal view of body abcut twice life size, showing characteristic cross bars of this race.

first, second, and third supralabials. Infralabials, mental, and chin shields whitish, unmarked, except as noted above. A pair of black occipital marks behind the parietals, two and a half scales long and seven scales high, separated on the median dorsal line by two scale rows, extending laterally to the level of the last infralabial.

Body brownish above with a pattern of seventy-six black crossbars about one-half scale wide, extending to the sixth scale row, becoming progressively fainter posteriorly. First three pairs of spots not fused to form crossbars. Diffuse lateral spots alternating with the dorsal crossbars, principally on the third and fourth scale rows; some of these joined with the dorsal crossbars. The black pigment forming these spots is on the skin between the scales and on the edges of the scales. The black markings obscure on the uniform brownish tail. The venter whitish, with the brown ground color of the dorsum tinting the edges of the ventars for a little less than the width of the first scale row; a very few faint small flecks of black along the lateral edges of the ventrals.

The hemipenis and dentition vary in no significant respect from *S. d. dekayi*.

Size.—The largest male specimen examined measures 350 mm., the largest female, 405 mm. The summary showing the geographic variation in maximum size, the average of adult specimens (those over 175 mm.) and the tail/total length ratio is given in Table 13.

VARIATION

Scutellation.—Sexual dimorphism in this race is like that of *S. d. dekayi*. The ventrals average slightly higher in the Mississippi Valley and there is a more pronounced trend toward a high number of subcaudals to the south as may be seen in Table 13. The sum of the ventrals and subcaudals exhibits this trend, the average exceeding 185 in the Florida panhandle. The extremes of ventrals in males are 119 to 133 (one hundred and fifty-three specimens), in females 125 to 140 (one hundred and fifty-two specimens). The extremes of subcaudals in males are 50 to 62 (one hundred and fifty specimens), in females 42 to 56 (one hundred and forty-seven specimens). The largest series from a single state, without other subspecies, is from Illinois. Ventrals in 43 males and 39 females range 121-131, average 126.3, and 127-140, average 132.7; in subcaudals, 43 males and 38 females range 50-61, average 55.4, and 42-51, average 47.4.

Variation in head plates is shown in Table 14.

Coloration.—Variation in coloration in this race is very much like that in *S. d. dekayi.* To the west this race intergrades with *S. d. texana,* which lacks the vertical dark bar on the temporal. While the temporal bar is highly constant over the wide range *S. d. wrightorum,* some specimens from northern Illinois and Indiana do not have it. These are included with subspecies *wrightorum* as they form only a minor portion of the population. The fusion of the dorsal spots to form short crossbars is somewhat variable in the north,

TABLE 13.—Summary of Regional Variation in Certain Characters of *Storeria dekayi wrightorum.*

	North Central			South Central			South Atlantic Coastal Plain		
	No.	Extremes	Av.	No.	Extremes	Av.	No.	Extremes	Av.
Ventrals									
Males	118	119-133	125.4	19	120-130	124.7	16	122-130	124.8
Females	105	125-140	132.0	34	126-138	131.9	13	127-134	130.7
Subcaudals									
Males	116	50-61	54.9	18	50-62	57.3	16	52-61	56.6
Females	103	42-53	47.6	31	44-56	49.3	13	43-56	48.6
Ventrals + Subcaudals									
Sexes combined	218	171-189	179.9	49	172-192	181.6	29	175-190	181.0
Ventrals — Subcaudals									
Males	115	62-79	70.5	18	60-76	67.5	16	63-75	68.2
Females	103	70-92	84.1	31	76-94	82.7	13	78-89	82.5
Total Length									
Males	99	350	268.5	10	313	247.4	10	311	262.0
Females	87	405	312.1	27	399	290.6	13	378	282.5
Tail/Total Length Ratio									
Males	116	18.1-25.8	23.9	17	18.6-26.8	25.0	14	23.1-26.0	24.7
Females	100	17.6-23.1	20.2	30	18.7-23.8	21.3	12	19.3-23.7	20.9

For "Extremes" under "Total Length" only the maxima are given. The average total length is derived from specimens over 175 mm. in length. (These are assumed to be mature.) Regions used may be outline as follows: North Central—Ontario to West Virginia and west to Iowa and Oklahoma; South Central — Tennessee and Alabama west to Arkansas and Louisiana; South Atlantic Coastal Plain — Virginia to Florida.

i.e., Ontario, Michigan, Ohio, Indiana and Illinois. Intermediate specimens with the fusion complete in varying degrees are characteristic of this area.

HABITAT

Storeria dekayi wrightorum is found in much the same habitat as *S. d. dekayi,* but there is frequent reference in the literature to aquatic or semi-aquatic habits. At Reelsfoot Lake, Tennessee, specimens were taken by myself in the relatively dry higher portion of an extensive swampy area. In urban situations it appears that its habitat is precisely like that of *S. d. dekayi* in the east.

TABLE 14.—Summary of Variation in Head Plates in 305 Specimens of *Storeria dekayi wrightorum.*

Supralabials	6/6	6–R	6–L	7/7	8–R	8/8	
Frequency in per cent	0.7	0.3	1.6	normal	0.7	0.7	
Infralabials	6/6	6–R	6–L	7/7	8–R	8–L	8/8
Frequency in per cent	1.6	1.0	0.3	normal	4.9	3.6	0.7
Preoculars				1/1	2–R	2–L	2/2
Frequency in per cent				normal	0.7	1.0	0.7
Postoculars	1/1	1–R	1–L	2/2	3–R	3–L	3/3
Frequency in per cent	1.3	2.3	1.6	normal	6.6	6.2	5.2
Anterior Temporals				1/1	2–R	2–L	2/2
Frequency in per cent				normal	3.6	0.3	0.3
Posterior Temporals	1/1	1–R	1–L	2/2	3–R	3–L	3/3
Frequency in per cent	2.3	4.6	3.6	normal	11.5	9.2	11.1

DISTRIBUTION

Storeria dekayi wrightorum ranges in the Atlantic coastal plain from southeastern Virginia and North Carolina south around the Appalachian highlands and north in the Mississippi basin. To the west it intergrades with *S. d. texana* from western Louisiana north to Nebraska. It intergrades with *S. d. dekayi* from Ontario to Illinois and south along the fringe of the Appalachian region and the interior low plateau.

LOCALITY RECORDS

Specimens examined as follows:

CANADA

ONTARIO: *Elgin County*—Southwold Tp., Talbotville Royal, ROMZ 2188. *Frontenac County*—Abbey Dawn, Kingston, ROMZ 2379. *Kent County*—Mitchell's Bay, ROMZ 4322. *Leeds County*—Wallace Island, Lansdowne, ROMZ 5115. *Middlesex County*—London, ROMZ 2077; Hyde Park, CNM 916. *Muskola County*—Lake Rosseau, ROMZ 4749. *Norfolk County*—Long Point, ROMZ 1999, 2001-2, 2049; Turkey Point, CM 21020, ROMZ 3799-3801. *Parry Sound County*—Pointe au Baril, MCZ 22806. *Peel County*—Georgetown, ROMZ 213. *Wentworth County*—Oaklands, Aldershot, CNM 1059; Hamilton, CNM 1383. *York County*—Toronto, ROMZ 2316-17, 2381, 2522, 2622, 2625, 2627, 2661, 4713, 4894, 5023; Highland Creek, ROMZ 3901; Etobicoke Tp., Lambton Mills, ROMZ 3891, 5043, 3676; Long Branch, ROMZ 3662-63.

UNITED STATES

ALABAMA: *Lee County*—Auburn, USNM 102589-90. *Mobile County*—FNB—, USNM 42542, 55925, 55927; near Mobile, UMMZ 84435. "Alabama," USNM 55926.

ARKANSAS: *Benton County*—Sulphur Springs, UMMZ 60108. *Carroll County*—USNM 55922. *Greene County*—three and one-half miles southeast of Paragould, UMMZ 71985. *Hempstead County*—UMMZ 84170. *Lawrence County*—Imboden, FMNH 12551. *Pulaski County*—Little Rock, USNM 55924. *Washington County*—Chert Hill, east of Springdale, CA 4760.

FLORIDA: *Escambia County*—Pensacola, MCZ 15713, USNM 2222, FNB—. *Gadsden County*—Chattahoochee, ERA 46B. *Liberty County*—Appalachicola River Bottom, UFC 561; five-six miles north Rock Bluff, UMMZ 72809.

GEORGIA: *Berrien County*—Nashville, USNM 10711. *Chatham County*—Savannah, ANS 5892. *Elbert County*—Huguenot, USNM 29606. *Fulton County*—MCZ 31843; near Atlanta, UMMZ 67818-22. *Hall County*—Gainesville, URMNH 6693. *Lincoln County*—Island above Price Island, USNM 92062. *Rabun County*—ERA 46A. *Warren County*—thirteen miles south of Thompson, FNB—. "Georgia," MCZ 275.

ILLINOIS: *Alexander County*—Cairo, FMNH 2129. *Calhoun County*—INHS 1741-42. *Champaign County*—Urbana, FMNH 13205. *Cook County*—Chicago, FMNH 717, 14813, 22770, USNM 6388, CA 1364; Elmwood Park, CA 5077; Evanston, MCZ 3269, 3272; Homewood, FMNH 22857, 17648, 7839, 8788, 12537, 13198; Lemont, FMNH 27700; Willow Springs, FMNH 22771-73, 19400; Braeside, FMNH 15699-15702, 15761; Beverley Hills, Longwood, FMNH 2495, 22774, 1930; Summit, FMNH 804; Berwyn FMNH 822; Riverside, FMNH 17132; Lambert, FMNH 27281; Pullman FMNH 2672; Edgebrooke, FMNH 3527, 2787. *DuPage County*—Downer's Grove, FMNH 12540; Ingalton, FMNH 22736-37. *Jackson County*—Murphrysboro, FMNH 18617, FNB—. *Jersey County*—four miles north of Grafton, INHS 1731-34. *Kankakee County*—Pembroke Tp., FMNH 19220. *Lake County*—Pistakee Lake, FMNH 13185. *McLean County*—Bloomington, UMMZ 32332. *Morgan County*—Meredosia, FMNH 27858-59, 3261. *St. Clair County*—CAS 13033; Belleville, USNM 8983, 8770. *Wabash County*—Mt. Carmel, USNM 12028. *Will County*—New Lenox, FMNH 2976. "*Lake-Cook*" *County* line, FMNH 22831-36; "Southern Illinois," USNM 4814.

INDIANA: *Boone County*—Lebanon, USNM 2137. *Carroll County*—Delphi, MCZ 360. *Kosciusko County*—Winona Lake, FMNH 747, 22764. *Knox County*—Wheatland, USNM 10653-55, 13358-59. *Lake County*—Clark Junction, FMNH 22761; Pine, FMNH 22762-63; just south of Pine, FMNH 2837; Clark Junction, FMNH 2194; Hesseville, FMNH 21707-11; Dunes Park, LMK 24530-34. *Marion County*—Irvington, USNM 17967; Indianapolis, FMNH 21572. *Porter County*—Tremont, CA 1982-83, 907-08; near Dune Park, FMNH 3440. *Posey County*—New Harmony, MCZ 125. *Starke County*—northwest corner of county, LMK 24536. *Jasper-Pulaski Counties*—Jasper Pulaski Park, LMK 24529, 24537-39. "two miles west of Woodville, LMK 24535; "Lake Maxintuckee," USNM 42589, 33529.

IOWA: *Blackhawk County*—Dunkerton, ISC 573. *Boone County*—Boone, ISC 2821. *Butler County*—one-half mile west Shell Rock, ISC 575. *Clayton County*—two miles southwest Garnaville, ISC 570. *Des Moines County*—Burlington, MCZ 80. *Lee County*—five miles north of Montrose, ISC 574.

KANSAS: *Miami County*—CA 5274. *Riley County*—CA 5275. "Fort Riley to Pike's Peak," ANS 5833-39.

LOUISIANA: *East Baton Rouge Parish*—Baton Rouge, FNB—. *Livingston Parish*—Colyell, CORNELL 8443. *Natchitoches Parish*—Creston, CORNELL 7361, 7370, 7377, 7387, 7355. *Orleans Parish*—New Orleans, USNM 4798b, 1120, 12904. *St. James Parish*—USNM 10211; near Gramercy, AMNH 53893. *St. Tammany Parish*—Bush, FMNH 25622. *West Baton Rouge Parish*—Lobdell, USNM 31666. "Louisiana," ANS 5886.

MICHIGAN: *Genesee County*—UMMZ 63435. *Gladwin County*—UMMZ 78163. *Iosco County*—Cooke Dam, UMMZ 59168. *Kalamazoo County*—Kalamazoo, PA 1252. *Lenawee County*—Morenci, UMMZ 40483. *Livingston County*—Portage Lake, UMMZ 74507. *Mecosta County*—UMMZ 63385. *Saint Clair County*—Port Huron,

USNM 2215. *Washtenaw County*—CM 5003, 5004; Ann Arbor, AMNH 36896, UMMZ 30382, 38919, 57069.

MISSISSIPPI: *Bolivar County*—Rosedale, CA 7375; two and one-half miles southeast Rosedale, CA 7079. *Coahoma County*—Moon Lake, AMNH 6555. *Coctaw County*—Ackerman, UMMZ 90109. *Hancock County*—Bay St. Louis, FMNH 2028. *Harrison County*—Biloxi, AMNH 46757. *Hinds County*—Jackson, UMMZ 86695. *Lawrence County*—Monticello, USNM 2226. *Madison County*—four miles east of Canton, CA 6137, 6719, 6810-19. *Rankin County*—two miles south of East Jackson, CM 19019. *Webster County*—Mathiston, FNB—.

MISSOURI: *Butler County*—near Keenar (near Poplar Bluff), UMMZ 77435-36. *Carter County*—Big Springs State Park, UMMZ 68957. *Crawford County*—USNM 33939. *Johnson County*—Montserrat, PA 2660. *Lincoln County*—Sheepscott Bay, Isle of Springs, USNM 31953. *St. Francis County*—USNM 55935. *St. Louis County*—USNM 55928, KU 1731; Creve Coeur Lake, CA 8511. *Stoddard County*—USNM 55932; four miles northwest of Advance, CA 8530-31. *Stone County*—USNM 44294. "St. Louis," USNM 7278.

NORTH CAROLINA: *Guilford County*—Greensboro, FMNH 37899. *Hyde County*—Lake Landing, CM 15140. *Jackson County*—Dillsboro, UMMZ 80997, 80999-81000. *New Hanover County*—Wilmington, USNM 26077, ZSP 593. *Swain County*—Cherokee, USNM 15577. *Wake County*—Raleigh, FMNH 2029, 22766.

OHIO: *Erie County*—Castalia, UMMZ 62658; Huron Tp., FMNH 2545; Sandusky, UMMZ 32782. *Lucas County*—Little Cedar Point, ISC 578; Toledo, CM 5276, UMMZ 75622. *Warren County*—Monroe, USNM 10665-66.

OKLAHOMA: *Bryan County*—UMMZ 86539. *LeFlore County*—Wister, CM 720, AMNH 4213. *McCurtain County*—UOMZ 2094. *Ottawa County*—Vicinity of Kansas, UMMZ 81327. *Tulsa County*—Tulsa, AMNH 43458. "Indian Territory, Neutral Strip," AMNH 3381.

PENNSYLVANIA: *Allegheny County*—Pittsburgh, USNM 1945; Wexford, CM 8874. *Lawrence County*—Newcastle, Big Run, CM 10576.

SOUTH CAROLINA: *Anderson County*—Portman Shoals, CLEM 108. *Beaufort County*—Hiltonhead, ANS 5889. *Charleston County*—Santee River, Hampton Plantation, CHM 37-74-10, 36-74-11. *Lexington County*—two miles southeast of Leesville, CM 9520. *Oconee County*—Clemson, CLEM 56. *Richland County*—Wateree River along US 76 about twenty-one miles east of Columbia, ZSP 594. "South Carolina," CLEM—.

TENNESSEE: *Chester County*—F. O. Bottom, Henderson, JBH—. *Decatur County*—Kelley's Island, Ohio River, MCZ 5717. *Hardeman County*—fourteen miles northeast of Bolivar, CA 7681. *Knox County*—Knoxville, UMMZ 66725. *Lake County*—Horse Island, CORNELL 2222; Hunting Club road to Hickman, CORNELL 2350. *Madison County*—five miles north of Jackson, UMMZ 72256. *Obion County*—Reelfoot Lake, UMMZ 74583.

VIRGINIA: *New Kent County*—near Lanexa, CM 13263.

WEST VIRGINIA: *Randolph County*—Elkins, CM 15642-43, 15652, 15655, 15666, 15792.

WISCONSIN: *Dane County*—Madison, UMMZ 57862. *Grant County*—near Potosi, UMMZ 69642. *Racine County*—Racine, USNM 1958-59.

Storeria dekayi texana Trapido, subsp. nov.

Texas Brown Snake

Figs. 45-50

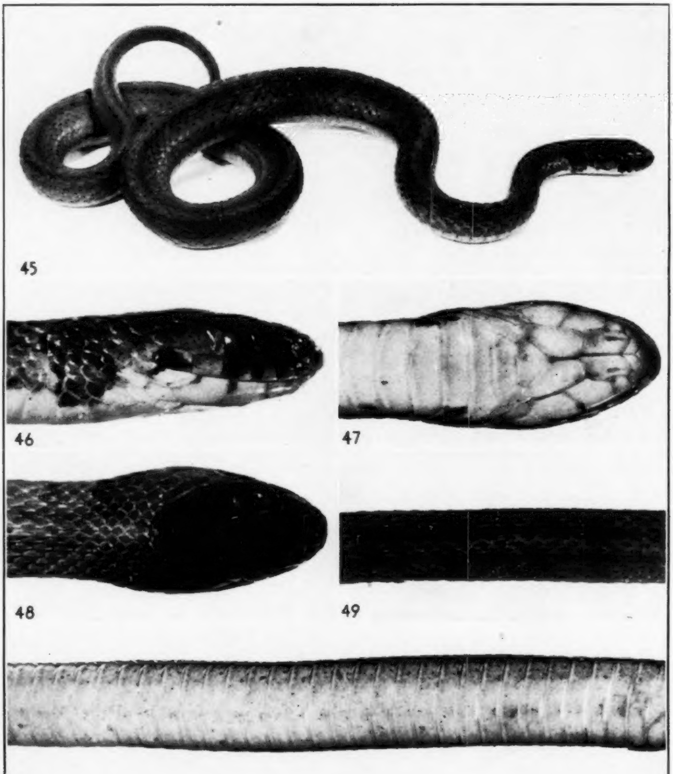
Storeria dekayi Baird and Girard, Cat. N. Amer. Rept. pt. 1, Serpents, p. 135 (partim), 1853; Cope, Rept. U. S. Nat. Mus., p. 1000 (partim), 1900; Ortenburger and Freeman, Pub. Univ. Okla. Biol. Surv., vol. 2, p. 185, 1930; Stejneger and Barbour, Check List N. Amer. Amph. Rept., ed. 4, p. 131 (partim), 1939.

Ischnognathus dekayi Boulenger, Cat. Snakes Brit. Mus., Vol. 1, p. 286 (partim), 1893.

DESCRIPTION

Holotype.—CORNELL 3530, adult female, taken at Edge Falls, four miles south of Kendalia, Kendall County, Texas, on June 16, 1942, by Albert J. Kirn. This is deposited in the collection of the Carnegie Museum at Pittsburgh, Pennsylvania.

Diagnosis.—This subspecies is characterized by the coloration of the anterior temporal which is not marked with a black vertical bar, nor with a longi-



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Figs. 45-50.—*Storeria dekayi texana*. All figures of Holotype, CORNELL 3530, photographed in life. Specimen from Kendall County, Texas. Fig. 45. Dorso-lateral view of whole animal, slightly reduced. Fig. 46. Lateral view of head and neck, several times life size. Fig. 47. Ventral view of head and neck, several times life size. Fig. 48. Dorsal view of head and neck, several times life size. Fig. 49. Dorsal view of body, slightly enlarged. Fig. 50. Ventral view of body, about twice life size.

tudinal stripe. The dark occipital blotches are broader than in other subspecies and the fourth labial is usually more extensively darkened.

Scutellation of Holotype.—Dorsal head plates normal; nostril opening in the anterior nasal, anterior and posterior nasals completely separated, subequal in size; preoculars single, higher than broad; postoculars two, the upper larger; anterior temporal single, longer than high; posterior temporals two on the right and three on the left; supralabials seven on each side, the fourth and part of the third entering the orbit; infralabials seven on each side, the fourth and the fifth are largest and subequal in size, others in descending order of size, six, three, one, seven, two, the first pair in contact on the median line behind the mental; mental triangular; chin shields in two pairs, subequal, the anterior pair in contact medially, the posterior with their rear half divergent and separated by a small scale; dorsal scales in seventeen rows, all keeled, the first row broadest, all except those of the first row emarginate posteriorly; apical pits not apparent. Ventrals 136, anal plate divided, subcaudals in 49 pairs.

Coloration of Holotype.—Head reddish brown, flecked with black above; right temporal clear, grading from reddish brown above to light brown below; left temporal similar, but with a black spot in upper rear corner. Nasals and oculars reddish brown flecked with black. Supralabials light brown marked with black as follows: the first with some dark in upper rear corner, second with black flecking along posterior margin, third with the posterior third black, fourth (below orbit) all black except anterior lower corner, fifth with anterior fifth black, sixth almost completely dark except for the anterior upper corner, seventh tipped with black anteriorly. Underside of head whitish except for a little dark pigment along the sutures of the infralabials.

A pair of dark occipital blotches uniformly three scales in width, separated on the median dorsal line by three scale rows and extending laterally to the edges of the ventrals.

Body brown above (with a faint cast of reddish in life), with faint black spots along the seventh scale row; these spots fainter posteriorly disappearing on the rear of the body and tail. No other lateral markings. Middorsal three scale rows slightly paler than the remainder of the dorsum. Venter whitish, tending to yellowish medially and to pinkish laterally. Brown dorsal pigment invading the lateral edges of the ventrals for a distance equaling about half the width of the lower scale row. Lateral edges of the ventrals very faintly flecked with black on the anterior part of the body.

Hemipenis.—The retractor penis muscle inserts in the region of the twenty-third subcaudal. The organ itself reaches the level of the eighth or ninth subcaudal. The spines and sulcus are like those in *S. d. dekayi.*

Dentition.—There are fourteen or fifteen teeth on the maxillary, as in *S. d. dekayi.* The dentary bears seventeen or eighteen teeth which gradually decrease in size posteriorly, the teeth somewhat more elongate than in *S. d. dekayi.*

TABLE 15.—Summary of Variation in Certain Characters of *Storeria dekayi texana.*

	Northern			Southern			Mexican		
	No.	Extremes	Av.	No.	Extremes	Av.	No.	Extremes	Av.
Ventrals									
Males	48	121-131	125.4	34	121-136	129.7	3	136-141	139.0
Females	44	125-140	131.1	58	123-143	134.5	2	138-141	139.5
Subcaudals									
Males	47	53-61	56.0	30	50-63	56.0	3	57-60	58.0
Females	44	41-51	45.5	58	38-52	46.8	2	48-49	48.5
Ventrals + Subcaudals									
Sexes combined	89	167-190	179.2	28	170-194	182.8	5	187-201	193.4
Ventrals — Subcaudals									
Males	46	62-74	69.1	28	64-82	73.6	3	79-83	81.0
Females	44	79-98	85.4	54	76-98	87.5	2	89-94	91.5
Total Length									
Males	42	341	251.0	25	316	246.0	1	313	313.0
Females	38	455	260.8	43	386	279.8	1	190	190.0
Tail/Total Length Ratio									
Males	46	23.4-26.9	25.1	28	22.8-26.9	24.7	3	23.2-23.6	23.3
Females	44	17.6-21.6	19.9	53	17.4-23.4	20.6	2	20.0-21.0	20.5

For "Extremes" under "Total Length" only the maxima are given. The average total length is derived from specimens over 175 mm. in length. (These are assumed to be mature.) Regions used may be outlined as follows: Northern—Iowa and Nebraska to Arkansas and Oklahoma; Southern—Mississippi, Louisiana and Texas; Mexican—San Luis Potosi and Hidalgo.

Size.—The largest male specimen measures 341 mm., the largest female 455 mm. The geographic variation in maximum length, the average length of adults (those over 175 mm.), and the tail/total length ratio are shown in Table 15.

VARIATION

Scutellation.—As in other members of the genus the ventrals are high in females, and the subcaudals high in the males. The number of ventrals in this subspecies increases toward the south, and is highest in Hidalgo and San Luis Potosi. While the counts in the Mexican specimens are high, they overlap the counts in specimens from Texas (see Table 15), so that with no supporting coloration differences, there is no reason for separating a further geographic race. There is less geographic variation in numbers of subcaudals, but also a slight trend toward an increase in the south. The figures for the sum of the ventrals and subcaudals (Table 15) also demonstrates the increase of linear elements toward the south. The summary of ventrals minus subcaudals in Table 15 emphasizes sexual dimorphism, while also showing the geographic trend expressed above. The largest series from a single state where no intergrades or specimens of other subspecies occur is from Texas. In 34 males and 56 females the range in ventrals is 121-136, average 129.7, and 123-143, average 134.5; in 30 males and 56 females subcaudals are 50-63, average 56.0, and 38-52, average 46.7.

Variation in the head plates is summarized in Table 16.

A somewhat obscure but none the less distinctive feature of this subspecies is the relative acuteness of the snout, especially in specimens from Texas. The internasals and prefrontals are slightly reduced, and the head when viewed from above is more pointed than in the relatively truncate snouted specimens from the north and east. In the ventral view the rostral projects beyond the lower jaw.

TABLE 16.—Summary of Variation in Head Plates in 189 Specimens of *Storeria dekayi texana.*

Supralabials		6-R	6-L	7/7	8-L				
Frequency in per cent		2.1	3.2	normal	1.1				
Infralabials	6/6	6-R	6-L	7/7	8-R	8-L	8/8		
Frequency in per cent	2.1	1.1	2.1	normal	0.5	2.1	1.1		
Preoculars				1/1	2-R	2/2			
Frequency in per cent				normal	0.5	1.6			
Postoculars	1/1	1-R	1-L	2/2	3-R	3-L	3/3	4-R	4-L
Frequency in per cent	1.6	2.1	4.8	normal	4.8	1.1	2.1	0.5	0.5
Anterior Temporal				1/1					
Frequency in per cent				all normal					
Posterior Temporals	1/1	1-R	1-L	2/2	3-R	3-L	3/3		
Frequency in per cent	2.6	3.7	4.2	normal	10.0	9.5	9.5		

Coloration.—The dorsal spots are discrete in *texana,* but from the eastern portion of the range (western Louisiana to Iowa) specimens are found with the unmarked temporal characteristic of this race, but with the dorsal spots

fused to crossbars. These are regarded as intergrades between *S. d. texana* and *wrightorum*.

While the temporal is typically clear and unmarked in *texana*, some individuals have a little black pigment along one of the margins of this plate, but neither the vertical dark bar of *wrightorum* or the longitudinal stripe of *temporalineata* is present. In other color features of the head, variation is like that of the races of *S. dekayi* already discussed, with the exception of the marking of the fourth supralabial (below the eye). Specimens of *texana* from Texas are almost invariably characterized by a black spot obscuring this scale, except for a narrow, light, labial margin. This is an extension of the wedge-shaped mark found on the fourth labial in *wrightorum* and *S. d. dekayi*. Along the southern Texas coastal strip this race intergrades with subspecies *temporalineata*, which characteristically has the labials unmarked except for a little dark powdering of the upper rear corner of the fourth supralabial. These intergrades are characterized by a reduction of the labial marks.

HABITAT

In Texas this race has been found under logs, boats, boards, and drift near lakes and streams.

DISTRIBUTION

S. d. texana occurs from Hidalgo in Mexico north through Texas to Minnesota. Its western limit coincides in general with the eastern edge of the Great Plains. On the east it intergrades with *S. d. wrightorum* from Iowa and western Wisconsin to western Louisiana. To the south it intergrades with *S. d. temporalineata* in the Mexican Gulf coastal plain.

The Mexican specimens are from the eastern border of the Sierra Madre Orientale, while in Texas this race occupies the coastal plain. To the north it occurs in the western portion of the central lowland.

LOCALITY RECORDS

Specimens examined as follows:

ARKANSAS: *Lafayette County*—Lewisville, KU 2489.

IOWA: *Boone County*—Ledges State Park, ISC 569. *Lee County*—five miles north Montrose, ISC 574.

KANSAS: *Barber County*—four miles north Lake City, USNM 94153-4. *Doniphon County*—UMMZ 59104. *Douglas County*—Lawrence, KU 1814. *Greenwood County*—eight miles southwest Toronto, KU 18016. *Kiowa County*—Rezeau Ranch, KU 21423. *Miami County*—UMMZ 66987. *Saline County*—Salina, CORNELL 3412. *Sumner County*—two miles northeast of Caford, FMNH 23370. *Wilson County*—Benedict, KU 18127.

LOUISIANA: *Cameron Parish*—UMMZ 86510. *Orleans Parish*—New Orleans, USNM 13090, 12922.

MINNESOTA: *McLeod County*—Winsted, USNM 65894.

MISSISSIPPI: *Harrison County*—Biloxi, UMMZ 76822.

NEBRASKA: "Fort McPherson," MCZ 3815.

OKLAHOMA: *Adair County*—four miles northwest of Watts, UOMZ 7215; vicinity of Kansas, UMMZ 81327. *Bryan County*—UOMZ 9912-14, 10037. *Caddo County*—Old Fort Cobb, USNM 11820, 11823. *Canadian County*—Devil's Canyon, UOMZ 13658. *Cleveland County*—UOMZ 12523, 12591, 12626, 13352-3, 13362, 77112;

near Norman, UOMZ 561, 3900, 8022, 8866, 9798, 19103, 20167, 22880-83, 22887, 22968. *Comanche County*—UOMZ 1722, 13129; Wichita National Forest, UOMZ 4015, 4385; W. Cache Creek, UOMZ 8215. *Craig County*—Vinita, Indian Territory, ANS 15516. *Garvin County*—Mayesville, UOMZ 10469-70. *Kay County*—Ark. River near Ponca City, OAM 190. *Latimer County*—near Wilburton, OAM 112, UOMZ 10106. *LeFlore County*—Wister, CM 718-19, 721-22. *Logan County*—Guthrie, UOMZ 11028; five miles north Edmond, UOMZ 18979. *McClain County*—five miles south Norman, UOMZ 10052. *McCurtain County*—UOMZ 17275; fourteen miles east Broken Bow, UOMZ 17562. *Murray County*—Arbuckle Mountains, UOMZ 12631. *Okmulgee County*—UMMZ 64573-75; Okmulgee, UOMZ 12412. *Osage County*—Ark. River region, ten miles east of Ponca City, UOMZ 22780. *Pawnee County*—*near* Quay UOMZ 7998-99. *Payne County*—Stillwater, OAM 48-328, 116, 310. *Pottawatomie County*—Shawnee, UOMZ 13566, 13797-99, 13801-03, 13567-77, 18806. *Seminole County*—Bowlegs, UOMZ 10166-67. *Sequoya County*—two miles northeast Gore, UOMZ 9005. *Tulsa County*—Tulsa, LMK 8115.

TEXAS: *Aransas County*—St. Joseph Island, off Rockport, UMMZ 72355. *Atascosa County*—FNB—, Benton, CM 18373, KU 8489. *Bee County*—Beeville, CA—. *Bexar County*—Helotes, ANS 12312; VonOrmy, CORNELL 1588; San Antonio, Medina River bottom near Blue Wing Lake, CORNELL 478; San Antonio, Brackenridge Park, FNB—; Leon Springs, CAS 31108. *Bosque County*—Clifton, CM 740; "Clifton?" CM 1028-32. *Callahan County*—Putnam, USNM 71754. *Cameron County*—EHT-HMS A481: Boco Chica near Rio Grande Mouth, CORNELL 630; Harlingen, USNM 103741; Brownsville, USNM 52281, 52284, FMNH 39610, EHT-HMS A480. *Comal County*—New Braunfels, USNM 17699. *Dallas County*—Dallas, ANS 12309, 10703, MCZ 2434. *Ellis County*—Waxahachie, FMNH 11866. *Falls County*—USNM 55912. *Frio County*—near Pearsall, EHT-HMS A479. *Gonzales County*—Ottine, CORNELL 3409. *Harris County*—Houston, ANS 10706, 12313. *Hidalgo County*—Edinburg, CORNELL 1602, CA 6534-54; FNB—, CORNELL 1602. *Kerr County*—four miles east of Kerrville, FMNH 30585. *Kleberg County*—FMNH 35920-21; Kingsville, CORNELL 3531, FMNH 38052-53. *LaSalle County*—near Cotulla, CORNELL 1761. *Matogorda County*—Bay City, CM 870-71; Deming's Bridge, MCZ 19896. *McLennan County*—Waco, USNM 55914, 14646, KU 11933; south of Waco, UMMZ 70130. *Medina County*—North Castroville, CORNELL 3411, 3532; Chican Lake, CORNELL 3533. *Nacogdoches County*—Nacogdoches FMNH 35046. *Palo Pinto County*—Palo Pinto, CORNELL 3430-31. *Travis County*—Austin, KU 13715. *Victoria County*—USNM 42286, 42290; Victoria, USNM 78611-18; Black Bayou, CM 784-93. *Walker County*—eight miles northeast New Waverly, CA 6290. *Williamson County*—Georgetown, MCZ 43917. "Wichita River," ANS 12306; "Texas?" ANS 12314; "Barnard Creek, west of Columbia," USNM 32802; "Texas," MCZ 306; "Brazos River," USNM 2095; "Seley," CM 770.

HIDALGO: Near Tianguistengo, EHT-HMS 16142-44, 16258.

SAN LUIS POTOSI: five miles south of Valles, District Ciudad de Valles, EHT-HMS 4662, 4664.

TAMAULIPAS: Metamoras, USNM 7279.

STORERIA DEKAYI TEXANA X WRIGHTORUM

IOWA: *Lee County*—five miles north of Montrose, ISC 574.

KANSAS: *Bourbon County*—UMMZ 66983. Cherokee County—KU 1733. *Chautauqua County*—Spring Creek, KU 1745. *Donphan County*—Donphan Lake, KU 2342. *Douglas County*—Lawrence, EHT-HMS A482-500; Twin Mounds, KU 2339. *Franklin County*—Ottawa, USNM 89175. *Graham County*—KU 1744. *Johnson County*—CM 5504. *Marshall County*—UMMZ 66986. *Miami County*—UMMZ 66987; Pigeon Lake, USNM 89177. *Pottawattomie County*—Flush, UMMZ 75621. *Riley County*—UMMZ 66984-5, URMNH 1168, FNB—, FMNH 18134; Manhattan, FMNH 18133, FNB—. USNM 89176; Junction Blue, Kansas River, UMMZ 64415. "Kansas," USNM 4653.

LOUISIANA: *Natchitoches County*—Natchitoches, UMMZ 71387; Creston, CORNELL 7367.

MISSOURI: *Cass County*—Freeman, PA 2663. *Carter County*—Big Spring State Park, PA 2312. *Jackson County*—USNM 55937-38; Sugar Creek, PA 2661, CA 10696; three miles east of Independence, CA 10697. *Jefferson County*—Wickes, USNM 55930. *Miller County*—USNM 55936. *Oregon County*—USNM 55931. *Stone County*—USNM 55933; Galena ANS 5883; Marble Cave, USNM 55934. *Vernon County*—Nevada, UMMZ 32330. *Warren County*—USNM 55929. "St. Louis," USNM 7278.

OKLAHOMA: *Cleveland County*—Norman, UOMZ 13756. *Latimer County*—near Wilburton, UOMZ 11314, 11360, 11397, 10104, 10105, 11084, 11684-85. *LeFlore County*—one and one-half miles east of Zoe, UOMZ 16789. *McClain County*—one-fourth mile south of Norman, UOMZ 18980. *Murray County*—Arbuckle Mountains, UOMZ 8915. *Okmulgee County*—UOMZ 1360, 64572, 64576-77, 22779. *Pottawatomie County*—Shawnee, UOMZ 13800, UMMZ 77538. *Tulsa County*—UOMZ 13564; Tulsa, UOMZ 13565, FNB (eight specimens).

WISCONSIN: *Dane County*—Madison, FMNH 12679, UMMZ 57861.

Storeria dekayi temporalineata Trapido, subsp. nov.

Mexican Brown Snake

PLATE 9, Figs. 51, 52

Storeria dekayi Garman, Mem. Mus. Comp. Zool., vol. 8, p. 31, 143 (partim), 1883; Yarrow, Bull. U. S. Nat. Mus., vol. 24, p. 130 (partim), 1883; Cope, Proc. Amer. Philos. Soc., vol. 22, p. 282, 1885; Ferrari-Perez, Proc. U. S. Nat. Mus., vol. 9, p. 187, 1887; Cope, Bull. U. S. Nat. Mus., vol. 32, p. 75 (partim), 1887; Cope, Proc. U. S. Nat. Mus., vol. 14 (883), p. 675 (partim), 1891; Cope, Ann. Rep. U. S. Nat. Mus., p. 1000-1003 (partim), 1900; Amaral, Mem. Inst. Butantan, vol. 4, p. 150 (partim), 1929; Stejneger and Barbour, Check List N. Amer. Amph. Rept., ed. 4, p. 131 (partim), 1939; Taylor and Smith, Univ. Kans. Sci. Bull., vol. 25, p. 249 (partim), 1939; Taylor, Herpetologica, vol. 2, p. 79, 1942.

Tropidonotus dekayi Garman, Bull. Essex Inst., vol. 16, p. 25 (partim), 1884.

Ischnognathus dekayi Boulenger, Cat. Snakes Brit. Mus., ed. 2, vol. 1, p. 286-287 (partim), 1893; Günther, Biol. Cent. Amer., Rept., p. 136 (partim), 1894; Werner, Zool. Jahrb., vol. 57, p. 38 (partim), 1929.

DESCRIPTION

Diagnosis.—Similar to *S. d. texana* but with a higher number of ventrals and subcaudals, the labials completely or almost completely unmarked, anterior temporal with a horizontal dark mark.

Holotype.—USNM 32148, adult female, San Rafael, Jicaltepec, Vera Cruz, Mexico, alt. circa 100 feet, collected July 2, 1896, by C. H. T. Townsend.

Scutellation of Holotype.—Dorsal head scales normal; rostral nearly twice as broad as high; nostril opening in the anterior nasal and with its posterior edge bordering the suture between the anterior and posterior nasals; nasals divided below the nostril, but no suture apparent above the nostril; preocular single, much higher than broad; postoculars two, upper twice as large as the lower; anterior temporal single, three times as long as broad; posterior temporals three; supralabials seven, two-thirds of the third and all of the fourth entering the orbit, the fifth and sixth largest; lower labials seven, the first two in contact behind the mental, the fourth and fifth largest; mental triangular; chin shields in two pairs, the anterior and posterior of equal length, in contact

except rear half of the posterior pair separated by a small scale; dorsal body scales emarginate posteriorly, apical pits not apparent, scales in seventeen rows except for the occiput where there are nineteen rows to a point opposite the sixth ventral, the second row on each side being dropped; first scale row about twice as broad as the others; all scales keeled; ventrals 138; anal plate divided; subcaudals in 47 pairs; tail terminating in a soft spine 2.5 mm. long.

Coloration of Holotype.—In alcohol the specimen is brownish gray. The dorsum of the head is irregularly spotted with black, this concentrated somewhat near the margins of the parietals, at the rear of the frontal, and medially on the prefrontals. The rostral, nasals, and internasals are unmarked. The anterior temporal bears a longitudinal black stripe covering its upper half. The upper labials are clear straw colored except for a faint dusting of dark on the upper rear corners of the third and fourth supralabials. The ventral portion of the head is whitish and unmarked. The occiput has faint paired spots, followed on the body by prominent paired black spots on the sixth and seventh scale rows, with faint smaller spots alternating on the third and fourth scale rows. The pattern becomes obscure posteriorly, but approximately eighty-two pairs of spots are distinguishable on the body. Ventrals clear and whitish medially, and diffuse pale gray laterally, exhibiting small black flecks toward the side of each ventral. These flecks are mostly arranged as a single pair on each ventral, but posteriorly become scattered or absent.

Dentition in Holotype.—Maxillary teeth apparently sixteen in number, recurved, and subequal in length. Dentary with about sixteen teeth decreasing in size posteriorly.

Size.—The total length of the holotype is 408 mm. of which the tail comprises 18.9 per cent. This is the largest female examined. The average length and average tail/total length ratio for this race are given in Table 17.

VARIATION

Scutellation.—In the only male of this species available for study, the subcaudals exceed those of all the females examined. The sum of the ventrals and subcaudals in the male specimen much exceeds that in the females. The sum of ventrals and subcaudals in this race is high, and represents the extreme in the clinal trend toward an increase in these elements toward the south. The variation in the head plates of this race is slight. The upper labials are usually 7/7, 7/6 in two specimens; lower labials 7/7 except in one with ?/8; preocular uniformly 1/1; postoculars 2/2 except in one with 1/2; anterior temporals 1/1 except in one specimen with 1/3. The posterior temporals are more often three than two: 2/2 in two, 2/3 or 3/2 in three, and 3/3 in four.

Coloration.—Typical specimens of *S. d. temporalineata* have the temporal dark stripe covering the entire upper half of the anterior temporal scale and lack the intense dark markings on the labials that are characteristic of the more northern races of *S. dekayi,* although there may be some faint suffusion of gray along the upper margins of the supralabials in this race. *S. d. temporalineata* has the dark occipital markings restricted to small spots only slightly

larger than those along the back. These characters are found in all specimens of *S. dekayi* from the Gulf coastal plain in Mexico. Certain of these distinctive characters are found in specimens from the Gulf coastal strip in the United

TABLE 17.—Summary of Variation in Certain Characters in *Storeriay dekayi temporalineata*.

	Males			Females		
	No.	Extremes	Average	No.	Extremes	Average
Ventrals	1	138	138	8	132-143	138.6
Subcaudals	1	56	56	8	42-52	47.1
Ventrals + Subcaudals	1	194	194	8	179-191	185.8
Ventrals — Subcaudals	1	82	82	8	80-101	91.4
Total Length	1	207	207	8	408	339.8
Tail/Total Length	1	23.2	23.2	8	18.7-21.5	19.7

States even so far north and east as Louisiana, with one such from the panhandle of Florida; such specimens are thought to represent intergradation with *S. d. texana* along the Gulf strip of Texas and Louisiana.

The characters of the subspecies *texana* contrasted with *temporalineata* are: a clear usually unmarked anterior temporal, a prominent black mark below the orbit covering almost all of the fourth, and adjacent portions of the third and fifth supralabials, a black mark on either side of the suture between the sixth and seventh labials, and irregular wedge-shaped black marks bordering the sutures of the other supralabials, as well as an extension of the occipital marks into heavy blotches. Where *texana* and *temporalineata* intergrade along the Texas coastal strip there is a mixing of characters. There is fortunately an adequate series of specimens from this region to show this transition from one condition to the other. Snakes from this area have a varying amount of black pigment along the upper edge of the anterior temporal, and some have this as well developed as pure *temporalineata* from far to the south in Vera Cruz. Specimens from the Texas coastal plain with the temporal stripe well developed may always be recognized as the supralabials are not unmarked as in pure *temporalineata*. It is quite probable that specimens meeting all the requirements of subspecies *temporalineata* will be found in southeastern Texas and the range of this race probably includes this area. Those of an intermediate nature as outlined above are best designated as intergrades between the two races.

HABITAT

No accounts of the habitat of this race is Tamaulipas and Vera Cruz are available although it is probable that it is found in much the same sort of place as *S. d. texana*. Taylor and Smith (1938), who record collecting three specimens of *S. dekayi* five miles south of Valles, San Luis Potosi, one of which has proved to be this race, report that the snakes were found in piles of driftwood near a river bank.

DISTRIBUTION

Storeria d. temporalineata occurs along the Gulf coast in Tamaulipas and

Vera Cruz. It probably extends inland to the base of the Sierra Madre Orientale and north to extreme southern Texas, and has been recorded from over five thousand feet in Puebla. It is probably principally a species of low elevations.

LOCALITY RECORDS

Specimens examined as follows:

TEXAS: "Texas," MCZ 15717.

PUEBLA: Puebla, UMMZ 85966.

SAN LUIS POTOSI: Five miles south of Valles, EHT-HMS 4663.

VERA CRUZ: La Palmilla, Canton of Jalacingo, AMNH 4292; San Rafael, Jacaltepec, USNM 32148 (HOLOTYPE); Jalapa, ANS 5885, MCZ 2843, 15990; "Vera Cruz," ANS 11675.

STORERIA DEKAYI TEMPORALINEATA X TEXANA

LOUISIANA: *Iberia Parish*—Avery Island, FMNH 34816. *Jefferson Davis County*—Jennings, CORNELL 7298-99. *Orleans Parish*—New Orleans, USNM 4798a; Gr. Coteau, New Orleans, USNM 5199. *Saint Mary Parish*—Morgan City, USNM 73828.

TEXAS: *Bee County*—Medio Creek near Beeville, OAM 809. *Brazoria County*—USNM 55913. *Cameron County*—USNM 17058-59; Brownsville, USNM 52300. *Hardin County*—Sour Lake, USNM 36389. *Harris County*—Houston, ANS 10705. *Matagorda County*—Bay City, CM 872.

TAMAULIPAS: Metamoras, USNM 7279.

STORERIA DEKAYI TEMPORALINEATA X WRIGHTORUM

LOUISIANA: *Orleans Parish*—New Orleans, USNM 15377. *Natchitoches Parish*—Creston, CORNELL 7364. "Louisiana," USNM 12923.

MISSISSIPPI: *Hancock County*—Bay St. Louis, FMNH 22768. *Harrison County*—Biloxi UMMZ 76823, 76821.

STORERIA DEKAYI ANOMALA Dugès
Orizaba Brown Snake

PLATE 9, Figs. 53-55

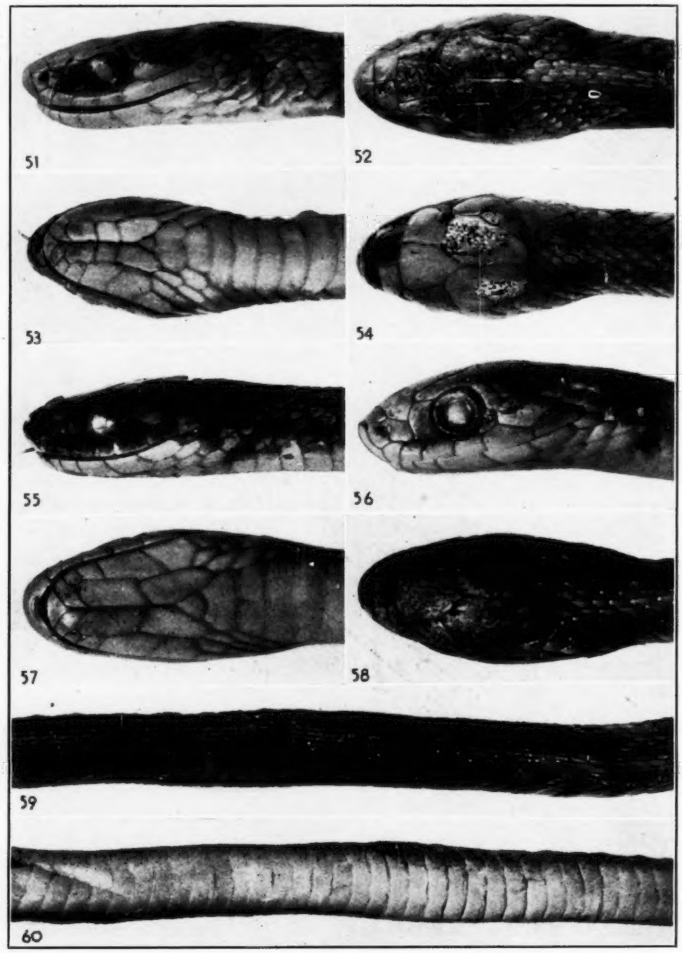
Storeria dekayi var. *anomala* Dugès, Proc. U. S. Nat. Mus., vol. 11, p. 9-10, figs., 1888; Dugès, La Naturaleza, (2), vol. 1, p. 401-2, figs., 1890; Bocourt, Miss. Sci. Mex., vol. 13, p. 744-745, 1893.

Storeria dekayi Yarrow, Bull. U. S. Nat. Mus., vol. 24, p. 130 (partim), 1883; Cope, Bull. U. S. Nat. Mus., vol. 32, p. 75 (partim), 1887; Dugès, La Naturaleza, (2), vol. 2, p. 481, 1896; Cope, Ann. Rept. U. S. Nat. Mus., pp. 1000-1003 (partim), 1900.

Ischnognathus dekayi Boulenger, Cat. Snakes Brit. Mus., ed. 2, vol. 1, p. 286-7, (partim), 1893; Günther, Biol. Cent. Amer., Rept. p. 136 (partim), 1894; Boulenger, Cat. Snakes Brit. Mus., ed. 2, vol. 3, p. 611, 1896.

Storeria dekayi anomala Taylor, Copeia, 1933, p. 97, 1933.

This subspecies was described as a "variety" of *Storeria dekayi*, with three pairs of chin shields instead of two. Cope (1900) considered this of no signifi-



Figs. 51-60.—All views slightly enlarged. *Storeria dekayi temporalineata*, Holotype, USNM 32148 from Jicaltepec, Vera Cruz. Fig. 51. Lateral view of head and neck. Fig. 52. Dorsal view of head and neck. *Storeria dekayi anomala*, Holotype, in Alfredo Dugès Museo, from Orizaba, Vera Cruz. From photograph by H. M. Smith. (The specimen was about to shed when preserved, scales are peeling off.) Fig. 53. Ventral view of head and neck. Fig. 54. Dorsal view of head and neck. Fig. 55. Lateral view of head and neck. *Storeria dekayi tropica*, Holotype, USNM 6759, from Peten, Guatemala. Fig. 56. Lateral view of head and neck. Fig. 57. Ventral view of head and neck. Fig. 58. Dorsal view of head and neck. Fig. 59. Dorsal view of body. Fig. 60. Ventral view of body.

cance as he had observed a partial splitting of the chin shields in specimens from the United States and Canada. The three chin shields, however, prove to be constant in specimens from the vicinity of Orizaba, and I have observed it in but one other of the hundreds of *S. dekayi* examined (a specimen from Louisiana, FMNH 34815). While the race has a restricted range, there seems no reason to question its validity.

Taylor (1933) found the type of *S. d. anomala* in the Alfredo Dugès Museo at the Colegio del Estado de Guanajuato, and Dr. H. M. Smith has kindly made available to me a redescription of the holotype from a manuscript on the Dugès types in the Guanajuato Museum by himself and Mr. Walter Necker, as well as photographs of the holotype.

DESCRIPTION

Diagnosis.—Similar to *S. d. temporalineata,* from which it differs in having three chin shields instead of two, as result of the transverse splitting of the anterior pairs; and in the somewhat more extensive occipital markings.

Scutellation of Holotype.—(From the manuscript of H. M. Smith and Walter Necker).

Head thick, not flattened; length of portion of rostral visible from above about half length of an internasal; median internasal suture somewhat less than median pre-frontal suture; maximum length of internasal about four-fifths that of pre-frontals; frontal pentagonal, its anterior edge somewhat curved, lateral edges somewhat convergent posteriorly, the angle posteriorly nearly a right angle (about 75 degrees); frontal longer (3 mm.) than wide (2.2 mm.), longer than its distance from tip of snout (2.4 mm.), shorter than parietal (4 mm.), equal to length of parietal suture; greatest width of a supraocular (0.9 mm.) somewhat less than half the width of frontal.

Nasal large, naris pierced nearer upper than lower edge, about in the middle anteroposteriorly; nasal suture complete below, but not above naris (a groove above, but definitely no suture); posterior section of nasal slightly larger than anterior; no loreal; one large preocular, about twice as high as long; pupil round; diameter of eye (1.7 mm.) less than its distance from tip of snout (2.6 mm.); two postoculars on one side, three on other, the upper largest; a small flat temporal, subequal in size to upper postocular, wedged between a single large anterior temporal and the fifth supraocular, narrowly in contact also with lower postocular (two lower, on one side) and sixth supralabial; excluding this small scale, the temporal formula on one side is 1-3-3, on the other 1-2-2; seven supralabials, third and fourth (also fifth, on side with two postoculars) entering orbit; fifth supraocular the largest and highest.

Mental triangular, with a labial border four-fifth that of rostral; seven infralabials, scales of the first pair in contact medially, fourth and fifth considerably larger than others, subequal; three pairs of chinshields, the anterior in contact with four supralabials, the middle with one (fourth), the posterior with two (fourth and fifth); posterior pair of chinshields largest, longest, somewhat divergent, divided posteriorly by a single small scale, broadly in contact anteriorly; median pair of chinshields narrower and shorter than others, nearly square; anterior pair of chinshields very slightly narrower than posterior, about two-thirds as long (anterior pair, 1.5 mm.; posterior pair, 2.2 mm.); two broad median scales between chinshields and first ventral.

Dorsal scales in 17-17-17 rows, all keeled, without apical pits, all distinctly although slightly notched at apex; scales of median row of dorsals smallest, the scales gradually increasing in size to the first (outer) row; the scales of this row are one and one-half times as large as the scales of the adjacent (second) row; ventrals 143 (a half ventral immediately precedes anal; this with another half ventral on the other side between the

12th and 13th ventrals are counted together as one)*; anal divided; subcaudals 45, divided; a terminal spine; female.

Coloration of Holotype.—(From the manuscript of H. M. Smith and Walter Necker).

The color of the specimen is obscured by the translucency of the old epidermis, which was apparently about to be shed when the snake was killed. The general ground color is a brownish slate; a series of very small, indistinctly outlined spots on each side, following the seventh scale row; these spots are most frequently placed on alternate scales; the anterior spot of each series, immediately posterior to the parietals and temporals, is considerably enlarged, covering parts of nine scales on one side, five on the other; the area between these series of spots, at least on the anterior third of the body, seems perceptibly lighter than the sides of the body.

The supralabials (except the upper edges of the first four) and the lower half of the large anterior temporal are lighter than the dorsal and the rest of the lateral surfaces of the head; the gular and lower labial regions are distinctly yellowish, with a slight orange tinge; the dorsal color encroaches slightly upon the ends of the ventrals and subcaudals; a series of very small black spots on each side, placed near the ends of the ventrals; this series extends from the gular region to the anus, the spots becoming indistinct near the anus; on some ventrals there are two small spots on a side, instead of one; otherwise the ventral surfaces of the belly and tail are pale yellow.

Hemipenis.—The penis retractor muscle inserts at the level of the twenty-second or the twenty-third subcaudal scale. The hemipenis itself is finely spinose as in other races of *S. dekayi* with one much enlarged basal spine, and two to several lesser ones clustered about it distally.

Dentition.—The maxillary is provided with fifteen slender recurved teeth, subequal in length. The dentary, in one specimen examined, bears sixteen teeth, decreasing in length posteriorly.

Size.—According to the manuscript of Smith and Necker the holotype measures 278 mm., of which the tail comprises 19.1 per cent. The total length and tail/total length ratio of other specimens examined are given in Table 18.

VARIATION

The variation in scalation in this race is shown in Table 18. The upper labials are uniformly 7/7; lower labials 7/7 in four specimens, 7/8 in USNM 110328; preocular uniformly single.

While the specimens available are few, it is apparent that there is a trend in this race toward the breaking up of the temporal plate anteriorly. The numbers of ventrals and subcaudals are about the same as in *S. d. temporalineata*. A specimen from Jalapa, Vera Cruz (MCZ 2843) has one of the anterior chin shields divided, the other entire. This intergrading specimen is included with *S. d. temporalineata*.

The coloration of *S. d. anomala* is similar to that of *S. d. temporalineata*, but the occipital spots are somewhat larger than in that race. All specimens examined had the horizontal dark stripe on the temporal, and the labials almost completely unmarked.

* Dugès' count is 145; he evidently counted with the ventrals the two scales between the chinshields and the scale I consider the first ventral (the first of full width).

HABITAT

Dugès (1888) found the type of this race, "sous une pierre, au bord d'un ruisseau, dans un endroit, extremement humide et d'une vegetation tropicale." Dr. H. M. Smith informs me that the specimen he took at Tequeyutepec was on a grassy hillside in a region of broken, hilly country.

DISTRIBUTION

Storeria d. anomala is known in a rather restricted area from Orizaba to Jalapa in west central Vera Cruz. Here it occurs in the foothill zone intermediate between the coastal plain to the east and the mountains bordering the central Mexican plateau to the west. One specimen bears the locality data, "Alpine Zone, Orizaba," but other specimens come from altitudes between 4500 and 5600 feet. Along the coastal plain it intergrades with *S. d. temporalineata.*

LOCALITY RECORDS

Specimens examined as follows:

VERA CRUZ: Jalapa, alt. circa 4490 feet, USNM 5565; Tequeyutepec, alt. circa 5600 feet, USNM 110328; Orizaba, USNM 8939; Orizaba, Alpine Region, USNM 7081.

STORERIA DEKAYI TROPICA Cope

Tropical Brown Snake

PLATE 9, Figs. 56-60

Storeria tropica Cope, Proc. Amer. Philos. Soc., vol. 22, p. 175, 1885; Bull. U. S. Nat. Mus., vol. 32, p. 75, 1887; Proc. U. S. Nat. Mus., vol. 14, p. 674, 1891; Ann. Rept. U. S. Nat. Mus., p. 1000, 1900.

Storeria dekayi Bocourt, Miss. Sci. Mex., vol. 13, p. 742-744 (partim), 1893; Amaral, Mem. Inst. Butantan, vol. 4, p. 150 (partim), 1929; Schmidt, Zool. Ser. Field Mus. Nat. Hist., vol. 22, p. 480, 1941; Schmidt and Stuart, Zool. Ser. Field Mus. Nat. Hist., vol. 24, p. 237, 1941.

Ischnognathus dekayi Boulenger, Cat. Snakes Brit. Mus., vol. 1, p. 286-287 (partim), 1893; Günther, Biol. Cent. Amer., Rept., p. 136 (partim), 1894.

Cope regarded the six supralabials and the absence of the dark vertical temporal bar as the characters distinguishing *S. tropica* from *dekayi.* The head plates of *Storeria* in Guatemala and Honduras are highly variable (see Table 19), and there can be no doubt that records of *S. dekayi* from Guatemala and Honduras are to be referred to *tropica,* the southernmost form in the *S. dekayi* cline.

The holotype in the United States National Museum (No. 6759) from Peten, Guatemala, is in good condition.

DESCRIPTION

Diagnosis.—This race is similar in essential features to *S. d. temporalineata* but differs in the lower average number of ventrals plus subcaudals (*temporalineata*=187: *tropica*=181), the lower average number of posterior temporals (*temporalineata*=2.6: *tropica*=2.0), and the reduced, more pointed snout.

TABLE 18.—Variation in Certain Characters of *Storeria dekayi anomala.*

Museum	No.	Sex	Ventrals	Subcaudals	Ventrals+ Subcaudals	Ventrals— Subcaudals	Post-oculars	Anterior Temporals	Posterior Temporals	Total Length	Tail/total Length
USNM	5565	♂	136	50	186	86	2/2	1/1	2/2	360	20.8
USNM	8939	♂	140	50	190	90	2/2	1/1	2/3	382	20.8
USNM	110328	♂	137	51	188	86	2/2	1/3	4/3	228	21.5
USNM	7081	♀	144	42	186	102	3/3	2/3	2/3	312	17.9
Dugès Museo (Holotoype)		♀	143	45	188	98	2/3	2/2	3/2	278	19.1

TABLE 19.—Variation in Certain Characters in *Storeria dekayi tropica.*

		Sex	Ventrals	Subcaudals	Ventrals+ Subcaudals	Ventrals— Subcaudals	Supra-labials	Infra-labials	Post-oculars	Posterior temporals	Total Length	Tail/total Length
FMNH	411	♂	125	55	180	70	7/7	7/7	2/2	3/2	300	23.7
FMNH	21796	♂	132	53	185	79	6/5	8/7	2/2	2/2	361	23.3
USNM	6759*	♂	132	53	185	79	6/6	7/7	3/2	3/2	341	22.6
FMNH	20527	♀	141	....	....	....	7/8	7/8	2/3	2/2	368	......
MCZ	38714	♀	134	44	178	90	7/7	7/..	1/3	2/2	348	19.3
MCZ	38715	♀	135	45	180	90	7/7	7/7	3/2	2/2	319	19.8
MCZ	38716	♀	133	....	....	....	7/7	7/7	2/2	2/2	273	......
USNM	35921	♀	135	45	180	90	7/7	7/6	2/3	1/1	185	18.9

* Holotype.

Scutellation of Holotype.—The dorsal head plates are normal, but the internasals are somewhat reduced in size; nostril between the anterior and posterior nasals; the nasals separated by a suture below the nostril but not above, posterior nasal larger than anterior; preocular single, higher than wide, postoculars three on the right and two on the left, the lowermost larger on the right, the upper larger on the left; anterior temporal single; posterior temporals three on the right and two on the left; supralabials six on each side (the normal sixth and seventh fused), the third and fourth entering the orbit; infralabials seven on each side, the fourth and fifth largest, the first pair in contact on the median line between the mental and anterior chin shields; the mental triangular; anterior and posterior chin shields subequal in length, in contact medially except for divergent rear half of the posterior pair separated by small scales anterior to the first ventral; scale rows 17-15-17 (the third scale row on each side is dropped from the fifth to the thirteenth ventral), all keeled, emarginate posteriorly, apical pits not apparent, the first scale row wider than the others.

Ventrals 132, anal divided, subcaudals divided, in 53 pairs.

Coloration in Holotype.—The top of the head weakly peppered with black; supralabials and infralabials whitish, clear and unmarked. A dark horizontal stripe on the upper part of the anterior temporal continuing forward onto the postoculars. Occipital marks reduced to the size of those of the back, which are principally on the seventh scale row. Approximately ninety pairs of spots on the body, with no fusion of the dorsal spots to form crossbars. Median three scale rows slightly lightened. Belly whitish with an occasional dark fleck laterally, and a faint suffusion of the dorsal brown onto the lateral margins of the ventrals.

Hemipenis in Holotype.—The hemipenis is about as in other races of *S. dekayi.* The retractor muscle inserts at the level of the twentieth subcaudal. The organ itself is finely spinose distally and has one much enlarged basal spine with three lesser ones distad.

Size.—The holotype, a male, measures 341 mm., the tail comprising 22.6 per cent. The largest male examined reaches the length of 361 mm., the largest female 368 mm. (See Table 19).

VARIATION

Scutellation.—The variation in scale characters of this race are given in Table 19. Sexual dimorphism is pronounced. The average of the sum of the ventrals and subcaudals most clearly shows the decrease from that in *S. d. temporalineata,* the adjoining race to the north. Variation in the labials is common in *tropica*. Seven is the normal number of both supralabials and infralabials, and it is evident that the six supralabials of the type, represents chance variation. The preoculars and anterior temporals are uniformly single. While the series of specimens of this race and of *S. d. temporalineata* available for study is small, there are trends toward differences in the number of postoculars and posterior temporals. Subspecies *temporalineata* has the postoculars almost uniformly two, while *tropica* often has an increase to three

(sometimes four, *fide* Bocourt, 1893). Conversely the average of the posterior temporal counts in subspecies *temporalineata* is 2.6 while in *tropica* it is 2.0.

Coloration.—Several of the specimens of this race examined have been darkened in preservation so that it is difficult to make out any pattern at all. As far as can be determined, however, the horizontal temporal stripe and the clear condition of the labials are constant. The occipital dark spots also seem uniformly reduced, as in the adjacent race, *temporalineata*.

HABITAT

The following information is from Karl P. Schmidt. *Storeria d. tropica* is an inhabitant of forested regions, and is a snake of the leaf mold ground cover. Field Museum No. 20527 was abroad on a path in a coffee plantation in the early forenoon.

DISTRIBUTION

This race ranges from Peten in northern Guatemala south and east to Yoro in north central Honduras. All records are from the Atlantic drainage. The known altitude range is from 2300 to 4300 feet.

LOCALITY RECORDS

Specimens examined as follows:

GUATEMALA

ALTA VERAPAZ: Samac,* near Coban, FMNH 20527; Senahu, USNM 35921.
PETEN: USNM 6759 HOLOTYPE.
GUATEMALA: FMNH 411.

HONDURAS

YORO: Subirana Valley, Yoro, FMNH 21796; Subirana Valley, Altitude 2300 feet, MCZ 38714-6.

AFFINITIES OF STORERIA DEKAYI

The *Storeria dekayi* complex appears to the writer to be derived from *S. storerioides*, or from the ancestral line of that species. The normal number of upper labials in these two species is seven, and the dorsal spot pattern, fusing to form crossbars, is also found in both. The ventral and subcaudal counts in *storerioides* are relatively high for the genus *Storeria*. The number of ventrals and subcaudals in *dekayi* is greatest in the area adjoining the range of *storerioides* (i.e., in that occupied by *S. d. temporalineata* and *S. d. anomala*). These snakes also average somewhat larger than other *Storeria dekayi*. Thus the *dekayi* series seems best read as a reductional sequence, from *temporalineata* and *anomala* through *texana* and *wrightorum* to *dekayi dekayi*. The genetic variability of *S. storerioides* might be expected to produce the mutation resulting in the three chin shields of *S. d. anomala*. It is thus significant that this race of *S. dekayi* is closest to *S. storerioides* geographically.

A difficulty in the interpretation of *S. dekayi* as a reduction series from *S. storerioides* lies in that there is an increase in number of scale rows from fifteen in *storerioides* to seventeen in *dekayi*. Thus *dekayi* is probably not a

* Also recorded from Coban by Bocourt (1893).

direct derivative of *storerioides*. It may be reasonable to suppose that *S. dekayi* is derived from a "pre-*storerioides*" stock with seventeen scale rows.

The head markings have proved to be of much value in working out the relations within *S. dekayi*. The temporal stripe, the clear labials, and the reduced occipital marks are essentially the same in subspecies *temporalineata*, *anomala* and *tropica*. *Storeria d. anomala* and *temporalineata* may be considered to be the closest of the *S. dekayi* line to the "pre-*storerioides*" stock. By reduction and some modification, *tropica*, to the south, was evolved from *temporalineata*. *Storeria dekayi texana*, with its clear temporal and spotted labials, exhibits characteristics of *storerioides* that differ from those of *temporalineata*. In other important features of coloration and scalation it is, however, close to *temporalineata*. Thus in the schema of the probable evolution in the genus, *texana* is placed in a questionable position. From *texana*, *wrightorum* is derived by the appearance of the fused dorsal spots and the development of a new feature, the vertical temporal bar. *Storeria dekayi dekayi* retains the temporal bar, but has the dorsal spots separate, and a reduced number of ventrals and subcaudals.

The relations of the various species and races of *Storeria* are summarized in the following diagram.

The Origin of Storeria

There remains the consideration of the origin of the genus *Storeria* as a whole.

In the discussion of the affinities of *S. storerioides* it has been pointed out that that species possesses the genetic potentialities of the other members of the genus, and is probably the nearest of the living forms to the ancestral line from which the group evolved. We may now seek the group from which *S. storerioides* and thus *Storeria* as a whole is derived. Unfortunately, the evidence available is only that derived from study of living forms. There is much evidence, from a morphological point of view, that *Storeria* is a reduced Natricine tribe. In such essential features as the divided anal plate, the keeled scales, the spinose hemipenis, and the single sulcus spermaticus, *Storeria* is like *Natrix*. The presence of a loreal in *S. storerioides* represents at least one character in transition between *Natrix* and the other members of the genus *Storeria*, which lack the loreal.

The writer* has shown the chromosome complement in *Storeria occipitomaculata* to be thirty-two (2n, male). Nakamura (1928) working with Asiatic *Natrix* (*N. tigrina*) found the diploid number in males to be forty. The morphology of the individual chromosomes also differs from that found in *Storeria*. This may indicate an important distinction between *Storeria* and *Natrix*; unfortunately there are no chromosome studies yet available of North American *Natrix*. The evidence from the chromosomes is best held in abeyance until further comparative studies can be made. Until that time the question of the origin and relations of *Storeria* must be held open.

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* In a paper read at the April 1942 meetings of the American Society of Ichthyologists and Herpetologists, as yet unpublished.

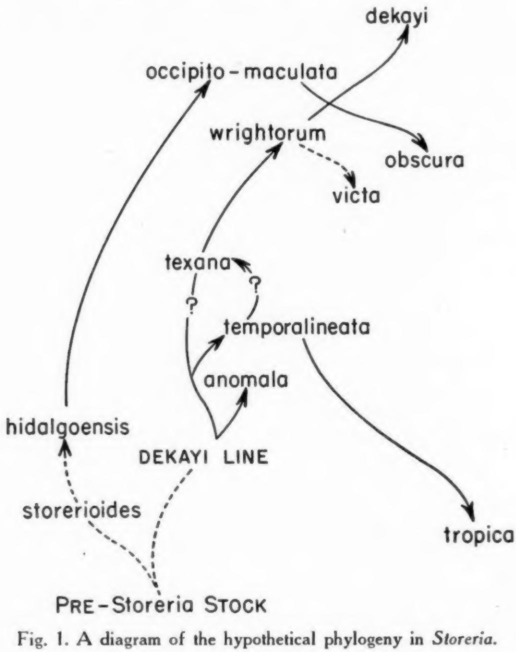

Fig. 1. A diagram of the hypothetical phylogeny in *Storeria.*

Postscript

Since the completion of this manuscript I have profited much by a discussion of the ranges of these snakes with Messrs. Karl P. Schmidt and Clifford H. Pope.

Mr. Schmidt has pointed out that the absence of records of *S. o. occipito-maculata* from what we may consider a steppe peninsula from central and southern Iowa and northern Missouri east through central Illinois and Indiana to Ohio (excepting the record from Menard Co., Illinois, whose authenticity he doubts) gives additional, though negative, evidence for the theory of the postglacial eastward extension of the steppe in North America. (See Schmidt, Ecology, 1938, **19**(3):396-407.) We might then judge that the moisture and cover requirements of this species which are met in the forested eastern regions did not become established in the postglacial times in the steppe peninsula soon enough for the entry of this species, which, failing to adapt itself, has never subsequently invaded this region, though it did move into the more suitable forested country to the north in Ontario, Michigan, Wisconsin and Minnesota.

Some explanation is also desirable with reference to the areas of overlap in the ranges of the subspecies of *S. dekayi.* The broadest area of overlap is

found between *dekayi* and *wrightorum* across much of Michigan, Ontario and Ohio. This area is one with no consequential physiographic barrier and a broad area of intergradation is not, therefore, unexpected. An examination of the records of specimens cited shows that individuals from this area have been placed in one subspecies or the other. Another author might have preferred to indicate all these specimens as "intergrades," but as individual specimens may be named as one race or the other, on the basis of the diagnostic characters, each specimen was recorded as of a particular subspecies. As the transition in color characters between *wrightorum* and *texana* in the region of the 95th meridian are more gradual certain individuals were considered intermediate, and they will be found to be cited as intergrades.

REFERENCES

(Only references in the text are included)

AMARAL, ALFRANIO DO. 1929—Estudos sobre ophidios Neotropicos. XVIII. List remissiva dos ophidios da regiäo Neotropica. Mem. Inst. Butantan **4**:i-viii, 129-271.

BAIRD, SPENCER FULLERTON AND CHARLES GIRARD. 1853—Catalogue of North American reptiles in the museum of the Smithsonian Institution. Part 1, Serpents. Washington: i-xvi, 1-172.

BROWN, ARTHUR ERWIN. 1904—Post-glacial nearctic centers of dispersal for reptiles. Proc. Acad. Nat. Sci. Phila. **56**:464-474.

BOULENGER, GEORGE ALBERT. 1893—Catalogue of the snakes in the British Museum (Natural History). London **1**:i-xiii, 1-448, pls.

BOULENGER, GEORGE ALBERT. 1896—Catalogue of snakes in the British Museum (Natural History). London **3**:i-xiv, 1-727, pls.

CARR, ARCHIE FAIRLY. 1940—A contribution to the herpetology of Florida. Univ. Fla. Pub., Biol. Sci. Ser. **3**(1):1-118.

COPE, EDWARD DRINKER. 1865—Third contribution to the herpetology of tropical America. Proc. Acad. Nat. Sci. Phila. **17**:185-198.

———1885—Twelfth contribution to the herpetology of tropical America. Proc. Amer. Philos. Soc. **22**: 167-194.

———1887—Catalogue of batrachians and reptiles of Central America and Mexico. Bull. U. S. Nat. Mus. **32**:1-98.

———1889—On the snakes of Florida. Proc. U. S. Nat. Mus. **11**:381-394.

———1891—A critical review of the characters and variations of the snakes of North America. Proc. U. S. Nat. Mus. **14**(882):589-694.

———1900—The crocodilians, lizards and snakes of North America. Ann. Rept. U. S. Nat. Mus. **1898**:153-1270, figs. and pls.

CORRINGTON, J. D. 1931—Abnormal herpetological specimens from Syracuse, New York. Amer. Nat. **65**(696):81-83.

DEKAY, JAMES EDWARD. 1842—Zoology of New York, reptiles and amphibia. pt. 3, Albany, N. Y.: i-vii, 1-98, figs.

DUGÈS, ALFREDO. 1870—Catáloge de animales vertebrados observados en la República Mexicana. La Naturaleza, **1**:137-145.

———1888—Sur deux espéces nouvelles des Ophidiens de Mexique. Proc. Amer. Philos. Soc. **25**:181-183, figs.

———1888—Description of Storeria dekayi, var anomala. Proc. U. S. Nat. Mus. **11**:9-11, 5 figs.

———1891—Description de la Storeria dekayi, var. anomala. La Naturaleza, ser. 2, **1**:401-402, pl. 27, fig. 12.

———1891—Dos Nuevas especies de ofidios Mexicanos. La Naturaleza, Ser. 2, **1**:402-403, pl. 27, figs. 13-14.

DUNN, EMMETT REID. 1936—The amphibians and reptiles of the Mexican expedition of 1934. Proc. Acad. Nat. Sci. Philad. **88**:471-477.

DUNN, EMMETT REID AND GILBERT C. WOOD. 1939—Notes on eastern snakes of the genus Coluber. Notulae Naturae **5**:1-4.

DUMÉRIL, A. M. C. 1853—Prodrome de la classification des reptiles ophidiens. Mem. Acad. Sci. Inst. France **23**:399-536.

DUMÉRIL, A. M. C. AND G. BIBRON. 1854—Erpetologie générale ou histoire naturelle complete des reptiles. Paris, **7**(1):i-xvi, 1-780.

FERRARI-PEREZ, FERNANDO. 1887—Catalogue of animals collected by the Geographical Exploring Commission of the Republic of Mexico. Proc. U. S. Nat. Mus. **9**:125-199.

GADOW, HANS. 1905—The distribution of Mexican amphibians and reptiles. Proc. Zool. Soc. London **2**:191-244.

GARMAN, SAMUEL. 1883—North American reptiles. Pt. 1, Serpents. Mem. Mus. Comp. Zool. **8**(3):1-185, pls.

———1884—The North American reptiles and batrachians. Bull. Essex Inst. **16**(1-3):3-46.

GÜNTHER, ALBERT CARL LUDWIG GOTTHILF. 1858—Catalogue of colubrine snakes in the British Museum (Natural History). London: i-xvi, 1-281.

———1885-1902—Biologia Centrali-Americana: Reptilia and batrachia. London: i-xx, 1-326, pls. The treatment of *Ischnognathus (=Storeria)* is contained in the signature dated July, 1894:129-136.

HALLOWELL, EDWARD. 1848—Description of a new species of Coluber inhabiting the United States. Proc. Acad. Nat. Sci. Phila. **3**:278-280, pl. 3.

HAY, OLIVER PERRY. 1892—Description of a supposed new species of Storeria from Florida, Storeria victa. Science **19**(479):199.

HOLBROOK, JOHN EDWARD. 1842—North American Herpetology. Philadelphia, J. Dobson, ed. 2, **4**:1-38, pls.

LOENNBERG, EINAR. 1894—Notes on reptiles and batrachians collected in Florida in 1892 and 1893. Proc. U. S. Nat. Mus. **17**(1003):317-339.

NAKAMURA, KENJI. 1928—On the chromosomes of a snake, Natrix tigrina. Mem. College Sci., Kyoto Imper. Univ., ser. B **4**(1):1-18, pls.

SMITH, HOBART M. 1939—The Mexican and Central American lizards of the genus Sceloporus. Zool. Ser. Field Mus. Nat. Hist. **26**:1-397, 59 figs., 31 pls.

———1940—An analysis of the biotic provinces of Mexico, as indicated by the distribution of the lizards of the genus Sceloporus. Sobretio An Esc. Nac. Ciencias Biol. **2**(1):95-110, map.

STEJNEGER, LEONHARD AND THOMAS BARBOUR. 1939—A check list of North American amphibians and reptiles. Ed. 4, Harvard Univ. Press: i-xvi, 1-207.

STORER, DAVID HUMPHREY. 1839—Reptiles of Massachusetts. Repts. Comm. Zool. Survey Mass. :203-253.

———1841—A report on the reptiles of Massachusetts. Boston Journ. Nat. Hist. **3**(1-2):1-64.

TAYLOR, EDWARD H. 1933—Notes on type specimens of reptiles and amphibians in the "Alfredo Dugès" Museum. Guanajuato, Mexico. Copeia (2):97.

———1941—Herpetological miscellany, No. II. Univ. Kans. Sci. Bull. **27**(7):105-139, text figs. and pls.

———1942—Mexican snakes of the genera Adelophis and Storeria. Herpetologica **2**(4):75-79.

TAYLOR, EDWARD H. AND HOBART M. SMITH. 1938—Miscellaneous notes on Mexican snakes, Univ. Kansas Sci. Bull. **25**(13):239-258, pl. and figs.

WRIGHT, ALBERT HAZEN AND SHERMAN C. BISHOP. 1915—A biological reconnaissance of the Okefinokee Swamp in Georgia. II. Snakes. Proc. Acad. Nat. Sci. Phila.: 139-192, pl. and figs.

YARROW, H. C. 1882—Check list of North American reptilia and batrachia, with catalogue of specimens in U. S. National Museum. Bull. U. S. Nat. Mus. **24**:1-249.

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The California King Snake: A Further Discussion

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Recently, Dr. Hobart M. Smith (1943) has reviewed the status of the longitudinally-striped California king snake, and has reached the conclusion that it is specifically distinct from the ringed form, although occasionally hybridizing with it. Thus he advocates a return to the nomenclature of Blanchard, Van Denburgh, and others, who referred to the striped snake as *Lampropeltis californiae,* and to the ringed form as *L. getulus boylii.* I have previously presented some data (1936, 1939), particularly on broods hatched in captivity, that appear to me to prove that these two forms are only pattern phases of a single subspecies, which should be called *L. getulus californiae.*

I should say at once that the older arrangement has the advantage of nomenclatorial simplicity. For if we consider the two forms, as they occur in San Diego County, to be pattern phases of a single species, how are we to designate the ringed form in those areas wherein the striped alternative is never found? Shall we consider it subspecifically distinct from the San Diego County snakes, based, not on any external character, but merely on its failure to produce pattern dimorphism? Yet in spite of the nomenclatorial clarity involved in Dr. Smith's proposal, I feel that his is not the correct interpretation. I think he has given inadequate weight to two important criteria, and I therefore renew the discussion. It is opportune also to present the statistics of the broods hatched in 1940-42.

For simplicity in these comments I shall follow Dr. Smith in grouping the aberrants, which I previously called "black ventrums" and "broken stripes," with the striped phase, thus considering only the "mixed striped and ringed" snakes, which I shall now call "mixtures," as true aberrants. I readily admit that there is no sharp line between any of these pattern phases, for borderline cases occur between any two; however, I think the geneticist will be concerned with the female sex-linkage evident in the "black ventrums," which suggests that they are as truly aberrant as the predominantly male "mixtures."

My first criticism of Dr. Smith's argument has to do with his statement that "free interbreeding of the *boylii* and *californiae* phases does not occur, else the hybrids would occur in a much greater proportion. Obviously there is very nearly complete physiological isolation of the two types where they occur together in the nearest approach to the pure state." This, it seems to me, places too much stress on the rarity of "mixtures" among the broods (and also in the wild population) and not enough on the mixed brood to be one divergent composition of the broods. If we consider a mixed brood to be one that contains any young differing in pattern from the mother (using Dr. Smith's simplified classification, which recognizes only three patterns instead of my five, i.e., "ringed," "striped," and "mixtures") we have the following classification of broods up to and including 1939:

Pattern of Mother	Composition of Brood Uniform	Mixed
Ringed	3	2
Striped	2	6

Adding the acquisitions of 1940-42, but omitting two broods in each of which only a single young snake survived, and two other broods (one mixed, one all striped) of which the mother's pattern was not recorded, we have the following:

Pattern of Mother	Composition of Brood Uniform	Mixed
Ringed	4	5
Striped	4	8

Thus, while "mixture" hybrids are comparatively rare, as Dr. Smith has said, mixed broods are common, representing no less than 61.9 per cent of the 21 broods upon which complete data are available. Under Dr. Smith's theory the fathers of these mixed broods must have had the opposite pattern from that of the mother, for otherwise either or both parents must have been heterozygous, thus immediately excluding the theory of separate species. Hence, it seems to me demonstrated that, as far as we may judge from a sample of 21 broods, free interbreeding does occur.

In fact, if mixed broods can result only from cross matings, it may be shown that such cross matings are even more frequent than would be expected were they to occur purely by chance without physiological barriers. I have previously pointed out that, in the coastal area of San Diego County, about 41.4 per cent of the king snake population is striped (or aberrant), the rest being ringed. With such a ratio we should expect about 51.5 per cent of uniform broods, whereas actually we had only 38.1 per cent in our sample of 21.[1] I should also point out that while no mixed broods could be changed in classification, had they been larger in number, the unmixed broods could have been, for the next youngster might have been of the opposite pattern.

Thus, continuing upon Dr. Smith's hypothesis, we are faced with the fact that cross mating is common and uninhibited, and that complete hybridization of the population would occur within a short time. The only alternative would be heterozygosity, which in itself involves the proof of my original conclusion. It will be noted that I have omitted discussion of the important point that these frequent cross matings (that is, cross matings in the light of Smith's theory) produce so large a proportion of non-aberrant and presumably homozygous young, which in itself would be most surprising. For example, this is quite different from conditions found among hybrid fishes, which usually have characters intermediate when compared with the parents. But this situa-

1 A 38.1-61.9 ratio is not significantly different, in a statistical sense, from a 51.5-48.5 proportion in a sample of 21 broods.

tion should be investigated by some geneticist, of which tribe I am not a member.

A second argument that may be advanced against Dr. Smith's theory is premised on the remarkable morphological similarity between the two phases, in all characters save that of pattern. With the advent of large enough samples of snakes from limited areas, we are becoming increasingly conscious of the considerable territorial differences that exist within a subspecies. These are usually below the level of nomenclatorial recognition, but they are nonetheless definite and real. With differences of this character within a subspecies, it is even more remarkable to find such a similarity in so many characters as exist between these two king snakes (Klauber, 1936:21) when we assume them to be separate species, even admitting their common ancestry as envisioned by Dr. Smith. For example, no two species of rattlesnakes or Pacific Coast garter snakes, with overlapping ranges, have anything approaching this morphological congruence. Such a coincidence in characters would be highly improbable, if resulting purely from chance.

Thus, I adhere to my former conclusion that this is a case of pattern dimorphism.

For the benefit of the geneticists who may be interested in this problem, I submit the following data on the 1940-42 broods. While the 1939 data were not included in the body of the previous paper (p. 13) they were given in a footnote on page 22.

		Pattern of Broods				
Number	Mother	Ringed	Striped	Mixed	Dark Ventrum	Broken Stripes
1940–7	Ringed	1				
1940–9	D. ventrum		1			
1940–11	D. ventrum				4	1*
1940–12–13	Striped		9			
1940–15	Striped	3	4		1	
1941–7	Unknown	3	3		1	
1941–8	Unknown		5		2	
1941–9	Ringed	4	3			
1942–1	Ringed	5				
1942–4	Ringed	7			3	
1942–6	Striped	2	2		2	1
1942–7	Ringed	3	1		2	

* This specimen also has a tendency toward a dark ventrum.

REFERENCES

KLAUBER, L. M. 1936—The California king snake, a case of pattern dimorphism. Herpetologica **1936**:18-27, 2 figs.

———1939—A further study of pattern dimorphism in the California king snake. Bull. Zool. Soc. San Diego **15**:1-23, 7 figs.

SMITH, H. M. 1943—Another analysis of the status of the western king snakes of the *Getulus* group. Amer. Midland Nat. **29**:245-251.

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Remarks on Hobart Smith's Analysis of the Western King Snakes

Ernst Mayr

Hobart Smith presents no original data in his re-interpretation of Klauber's analysis of the taxonomic status of the striped king snakes of California. Rather, he applies to the published data a set of taxonomic criteria that differs from those of Klauber, and comes on this basis to the conclusion that the two color patterns are not the phases of a dimorphic species, as Klauber had shown, but rather that they represent two valid, separate species. It is apparent, therefore, that the herpetological facts are not under discussion, but rather certain basic taxonomic concepts, which can be discussed by any taxonomist, be he a herpetologist or not. I am induced to examine Smith's interpretation in the hope of clarifying these taxonomic concepts, and of preventing other taxonomists from committing similar mistakes. The fallacy of some of Smith's reasoning cannot be too strongly emphasized. It is based on the same erroneous assumptions that have so often in the past misled other taxonomists.

Smith's two main reasons for maintaining the specific status of the striped king snakes of San Diego County are:

(1) Because the striped specimens do "not breed uniformly with the . . . coincident race" of the ringed specimens.

(2) Because the striped specimens are "much more radically different" from the ringed ones than are the various subspecies of the ringed "species."

It seems to me that both of these assertions are erroneous. The first is based on two fallacies. To begin with, Smith bases his conclusions on individuals rather than on populations. Instead of speaking of striped individuals, he speaks of *californiae* as a taxonomic unit. Taxonomic units, however, are based on populations and not on individuals. It should have been Smith's first task to prove that the striped individuals belong to a different population group than the ringed ones, but he fails to supply this proof. The second mistake is based on a misinterpretation of the significance of intergradation or "blending," as Smith calls it. Intergradation is one of the most misunderstood of all taxonomic criteria. The presence of complete intergradation may prove conspecificity or even complete taxonomic identity, but the absence of intergradation proves nothing *per se*. Males and females of most species are not connected by intergradation except where intersexes are known. The same is true for the phases of nearly all polymorphic species and particularly by those with a simple monogenic basis. Intergradation between alternative Mendelian types is frequently absent. Such cases have been reported so commonly in the recent taxonomic and genetic literature that it is hardly worth while to quote instances. To be sure, such cases have been confusing to those taxonomists

who attach a species name to every morphological or color variant. I might refer only to the *Rana burnsi* mutation of *Rana pipiens* (Moore, 1942), or to the white phase of many yellow butterflies, or to literally hundreds of similar instances listed in the recent textbooks of Goldschmidt, 1940; Mayr, 1942; and Huxley, 1943.

Smith's second argument, stating that the striped individuals are more different from the ringed ones than the various races of ringed king snakes, is already partly answered by the above quoted references. There are many cases known in the genetic literature in which a single mutation produces a much greater morphological effect than is shown by the average difference between two species. As a matter of fact, Smith's statement is not correct. The ringed and striped individuals of the San Diegan king snakes, according to Klauber, are identical in all their taxonomic characteristics except for the single character of pattern, while there are numerous differences of size, proportion, scutellation, etc. between the various ringed subspecies.

The blunt statement is made (p. 247) that "It is apparent that free interbreeding of the *boylii* and *californiae* phases does not occur, else the hybrids would occur in a much greater proportion. Obviously there is a very nearly complete physiological isolation of the two types, where they occur together in the nearest approach to the pure state." He continues to say that if there were free interbreeding of the striped and ringed individuals it "would probably result in prompt loss of identity of the two types and a uniform diffusion of the new characters throughout the whole area occupied by the parent population. Therefore, we are faced with the necessity of calling *californiae* a species different from *boylii*." With this statement Smith apparently returns to the pre-Mendelian concept of blending inheritance. It apparently does not occur to him that characters can be inherited in a strictly alternative manner, without any "loss of identity."

Smith says that "a partial mixing of the two species" is indicated by the rare occurrence of aberrant intermediate types between the striped and ringed patterns, comprising about 5.7 per cent of the total population. This interpretation again is in conflict with the facts. According to Smith, one would expect intermediates to result from the mating of all striped and ringed individuals, except where one of the parents is a homozygous dominant. Actually, Klauber's data show that there is a good deal of simple segregation of the two patterns indicating a simple Mendelian difference.

Of course, this still leaves the question to be answered what the aberrants are. It seems to me that the evidence indicates that these individuals are caused by the presence of additional modifying genes. There is certainly nothing to indicate that they are hybrids between the striped and ringed individuals.

The problem of the conspecificity of the striped and ringed individuals involves the following two questions.

(1) Are both patterns members of the same interbreeding population?

(2) Is there any evidence for a mating preference between individuals of the same color pattern?

The preceding contribution by Klauber and the analysis below by Dunn give a partial answer to these two questions.

There is one more point that requires comment. Smith bases some of his conclusions on the fact that he does not consider the striped pattern "a dominant type." It is not clear what he means by this statement. The word dominant may have one of three meanings. A character can be dominant in a strictly genetic sense meaning that heterozygotes will have the phenotype of the dominant gene. It may be used in a statistical sense indicating a numerical predominance of a phenotype in a given district. It may also refer to its ecological status, that is to its survival value, and such a type will be statistically dominant under most environmental conditions. It should not be forgotten that statistically or ecologically dominant types may be genetically recessive. It cannot be concluded from the fact that a phenotype is genetically or statistically dominant that it is expanding and spreading. Neither can the conclusion be drawn that its range is contracting even if a lack of dominance should be demonstrated. Even recessive genes may be spreading rapidly if they have a high survival value.

One can summarize this discussion by saying that not one of Smith's arguments in favor of a specific status for the striped phase of the California king snake seems to be valid. On the other hand there are at least three strong evidences in favor of considering the two phases as belonging to one species: (1) the simple segregation of the two patterns in most mixed broods, (2) the numerical frequency of the two phases in the progeny of ringed mothers as expected on a basis of random mating, and (3) the identity of the two phases in all characters except the color pattern.

I limit myself to a discussion of these questions, which seem to me basic. There are still a number of obscure points in regard to the status of these king snakes. The exact genetic basis of the two patterns is still unknown, though it is obvious that only very few genes can be involved. It is still somewhat dubious what nomenclature to apply, though this difficulty is lessened if we think in terms of populations rather than individuals. There is still the question of why the ratios of the various patterns of the wild-caught specimens differ from those of the broods born to striped mothers in captivity. There is still the question of why the aberrant patterns are more common in some districts than in others. These are questions that can be solved only by further collecting and by the breeding of these snakes in captivity; but none of these difficuties can be considered as being evidence against the conspecific status of the striped and the ringed phases of the California king snake.

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The Possible Genetic Basis of the Ringed and Striped Patterns[1]

L. C. DUNN (as communicated to E. MAYR)

Three sets of data are available that permit a preliminary genetic analysis of the dimorphism of the California king snake. One is the proportion of ringed and striped individuals among 1739 king snakes taken in the cismontane region of San Diego County, California, over a sixteen year period. A second consists of data for 140 juveniles under 500 mm. in length segregated from the previous sample. Klauber (1939: 11) notes that these juveniles represent a presumably unbiased sample whereas the larger sample may have been biased by his efforts to retain aberrant material. The third set of data is given by the broods of king snakes born in captivity from mothers of known phenotype taken in San Diego County (the pattern of the father of all being unknown). I have summarized this information in the following tabulation (Tables 1-3). Aberrant types (black ventrum and broken stripes) are included with the striped pattern of which they seem to be a modification. These data are taken from Klauber's paper of 1939, to which are added unpublished data from the seasons 1940-1942 (Klauber, *in litt.*).

TABLE 1

	Ringed		Striped and Aberrant		Total
	no.	%	no.	%	no.
San Diego County sample	1020	58.6	719	41.4	1739
San Diego County juveniles only	76	54.3	64	45.7	140

TABLE 2

	Broods	
Ringed mothers	Ringed	Striped and Aberrant
1935-8	22	2
1939	2	2
1940-2	20	9
	44	13
	77.2%	22.8%
Striped mothers		
1935-8	3	20
1939	4	13
1940-2	5	19
	12	52
	18.8%	81.2%

1 No breeding experiments have so far been undertaken to determine the genetic basis of the difference between the striped and the ringed pattern of the California king snake. It is therefore unknown whether this difference depends on a single or on several genetic factors, or (if there is a simple genic difference) whether the gene for striped or ringed is dominant. However, it seemed to me that enough was already known about the occurrence and the distribution of the two patterns to permit a rough analysis. Dr. L. C. Dunn, Columbia University, New York, kindly undertook such an analysis and communicated the following results to me.—ERNST MAYR.

TABLE 3

	San Diego County sample	San Diego County juveniles	All broods
Ringed	58.6	54.3	39.5
Striped	41.4	35.0	36.1 (60.5%)
Aberrant		10.7	24.4
	100.0%	100.0%	100.0%

I tried to fit these data to the assumptions:

1. That the ringed and striped phases are differentiated by a single pair of Mendelian factors.

2. That mating is at random and viability equal for the several color phases.

3. That the distribution of the assumed pair of genes in nature can be determined from the frequency of striped (including aberrant) and ringed specimens in the population of cismontane San Diego County.

According to these assumptions either the ringed or the striped gene is a simple dominant. For example, if we assume that the striped gene is dominant, it would mean that among the observed striped snakes there are individuals which are homozygous for the striped gene (AA) and such that are heterozygous (Aa). This means that the proportion of the striped and ringed individuals in the population is not the same as the proportion of the genes on which the difference is based. The recessive gene (a) is actually much more common than is indicated by the occurrence of its homozygous phenotype (aa). The actual frequency of the two genes can be determined with the help of Hardy's equilibrium formula:

$$q^2AA : 2q(1-q)\ Aa : (1-q)^2aa$$

This formula applied to the juvenile king snake of San Diego County permits the following calculations:

San Diego County juveniles
(Sample 2, Table 1)

.55 Ringed
.45 Striped and Aberrant.

If we assume that the gene that controls the ringed pattern is recessive, then

$$\begin{aligned} \text{Ringed} = aa = .55 &= (1-q)^2 \\ \text{If } (1-q)^2 &= .55 \\ 1-q &= \sqrt{.55} = .74 \\ q &= .26 \\ 2q\ (1-q) &= .38 \end{aligned}$$

The distribution of the two genes in San Diego County juveniles would then be as follows:

TABLE 4

$q^2 = .0669$	AA= 6.7%	Striped
$2q\ (1-q) = .3831$	Aa=38.3%	Striped
$(1-q)^2 = .5500$	aa =55.0%	Ringed
1.0000	100.0%	

Table 4 gives the probable gene frequency for the population of San Diego County juveniles. This frequency can be utilized to calculate the probable proportion of the various gene frequencies among the broods of female snakes. Assuming random mating the frequency of the various combinations should depend on the gene frequency in the population. The following table can be constructed (Table 5).

TABLE 5

Mothers \ Fathers	AA .07	Aa .38	aa .55
.07AA	.005 AA	.027 AA+Aa	.038 Aa
.38Aa	.027 AA+Aa	.108 AA+Aa .036 aa	.104 Aa .104 aa
.55aa	.038 Aa	.104 Aa .104 aa	.303 aa

Based on the juvenile population of San Diego County and assuming the ringed phase to be recessive.

Since AA and Aa individuals have the same phenotype, it can be seen from Table 5 what the proportion of the two different phenotypes, namely aa and AA+Aa, is among the descendants of each class of females. Assuming the fathers to be represented in the proportion of .07 AA: .38 Aa: .55 aa, the expected progeny of aa mothers is .038 Aa+104Aa=.14 Aa, and .104 aa+.303aa=.41aa. The expected ratio among the progeny of the AA and Aa mothers can be computed in similar manner. This information is summarized in Table 6.

TABLE 6

San Diego County Juveniles

Expected ratio among progeny of aa mothers

.14	Aa	=	25.5%
.41	aa	=	74.5%
.55			100.0%

Expected ratio among progeny of AA and Aa mothers

.31	AA + Aa	=	69%
.14	aa	=	31%
.45			100%

TABLE 7

Broods from Ringed mothers

	Ringed	Striped	
actual no.	44	13	
actual %	77.2	%22.8	
Expected if ringed = aa	74.5%	25.5%	based on San Diego County juveniles
Expected if striped = aa	73. %	27. %	
Expected if ringed = aa	77. %	23. %	based on larger San Diego Co. sample
Expected if striped = aa	75. %	25. %	

Broods from Striped Mothers

	Ringed	Striped	
actual no.	12	52	
actual %	18.7	%81.2	
Expected if ringed = aa	31. %	69. %	based on San Diego County juveniles
Expected if striped = aa	33. %	67. %	
Expected if ringed = aa	34. %	66. %	based on larger San Diego Co. sample
Expected if striped = aa	36. %	64. %	

The next question to be answered is how the calculated ratios of Table 6 agree with the actually observed ratios of the broods that were born in captivity. The expected ratios can be calculated either by assuming that the aa (=recessive) individuals are ringed or that the aa individuals are striped. Both sets are included in Table 7. This table also contains a calculation based on the observed frequency of the two phenotypes in the larger San Diego County sample (Klauber 1939, see above Table 1, first sample).

The calculated figures show that ringed mothers should have an excess of ringed young and striped mothers of striped young. The actually observed frequencies agree with this prediction. Moreover the progeny of ringed mothers occur in about the proportions calculated on the assumption of random mating and a single gene difference. This result appears to justify the

inclusion of the aberrant patterns among the striped as was done by Klauber because of the resemblance of the aberrant to the general features of the striped form. One can now say that such a classification leads to reasonable and consistent gene frequencies suggesting that aberrants have the same main gene, possibly with different modifiers. There seems to be no indication that aberrants are hybrids.

The progenies from striped mothers do not fit the calculated frequencies very well. There is a serious deficiency of ringed offspring in such broods. One might suppose that such mothers came from a locality where striped males were more frequent, although there is, of course, no direct evidence for this. Preferential mating might cause such a discrepancy but it would have to be preference of striped mothers for striped males. Discrepancies may also arise if the effective breeding population (the potential number of mates) is small. But the evidence is at present too scanty to support speculation.

The data which are available at the present time contain at least three unknown variables, (1) the genetic basis of the striped and ringed patterns, (2) the relative viability of the genes controlling these patterns, and (3) the degree of random mating between individuals of the two pattern phases. Hardy's equilibrium formula is useful to test the assumption of Mendelian segregation, if one can be sure of random mating and of equal viability of all classes. Conversely, if one is sure of Mendelian segregation, one can use the formula to test whether random mating occurs. But if both of these factors are variables, one of the two cannot give a clear answer about the other.

The fact that there is a simple segregation — striped: ringed — among the young of so many of both the ringed and the striped mothers indicates a simple Mendelian basis for the difference between the two patterns. The discrepancy between the expected and observed frequencies of pattern types among the progeny of striped mothers seems, however, to be due to the interference of some additional natural factors.

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REFERENCES

MAYR, ERNST. 1942—Systematics and the origin of species. Columbia Univ. Press, New York: xiv + 334, 29 figs.

MOORE, J. A. 1942—An embryological and genetical study of *Rana burnsi* Weed. Genetics **27**:408-416, 2 figs.

SMITH, H. M. 1943—Another analysis of the status of the western king snakes of the Getulus group. Amer. Midl. Nat. **29**:245-251.

A Key to the Anopheles of the Southeastern United States, by Male Genitalia (Diptera, Culicidae)

Louis M. Roth[1]

Of the eleven different genera of mosquitoes known to occur in Southeastern United States, those species belonging to the genus *Anopheles* are of most importance to man. The females of this group of insects carry and transmit the protozoan parasites responsible for human malaria. In the Southeast *Anopheles quadrimaculatus* Say is the only important vector of malaria. However, almost all of the other anophelines recorded from this part of the country have been experimentally infected with one or more of the different species of malaria parasites, and some have been found naturally infected in the field. Therefore, until further studies are made, it might be well to consider most of the anophelines as potential malaria vectors. Simmons and Aitken (1942) have reviewed the natural and experimental infectivity of the different species of *Anopheles* with malaria parasites.

Ten species of *Anopheles* have been found in the Southeast and are distributed among nine of the southern states as shown in Table 1. All but one species belong to the subgenus *Anopheles*. *Anopheles albimanus* Wied., the only species of the subgenus *Nyssorhynchus*, was recorded once from Florida in 1904, but apparently did not become established. This species is chiefly a tropical one but occurs also in the lower Rio Grande Valley of Texas.

Three anophelines, previously considered varieties of *A. crucians* Wied. (King, 1939), have recently been recognized as distinct species (King and Bradley, 1941). These three forms, *A. crucians*, *A. bradleyi* King and *A. georgianus* King are very similar in the adult stage but differ in larval and pupal characteristics. Their genitalia show only slight differences. Unfortunately very few male specimens of *A. georgianus* and *A. bradleyi* were available to the writer and therefore a comparative study of a large number of these two species could not be made. It is quite possible that a thorough study of a large series of genitalia of these two species, together with *A. crucians* will yield more distinguishing characters than those now available in the literature. In the present paper these three forms will be considered as distinct species

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[1] Second Lieutenant, Sanitary Corps, Army of the United States.

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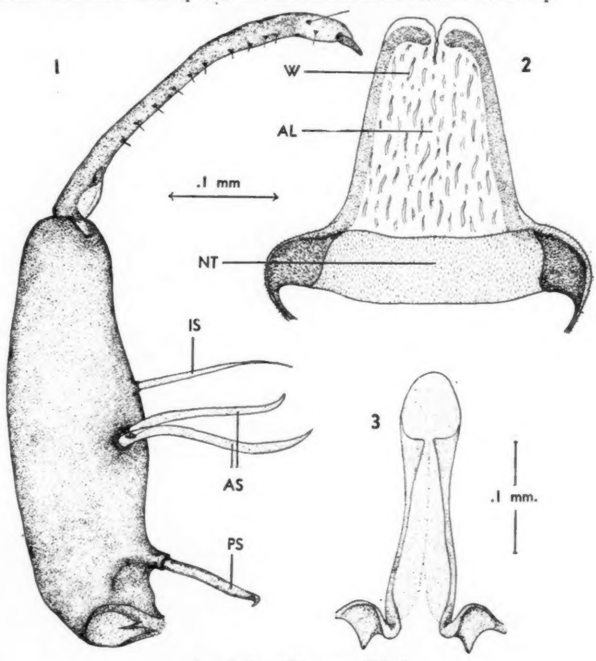
TABLE 1.—Distribution of the species of *Anopheles* in the Southeastern United States.

Species	Recorded from[2]								
	Fla.	Ga.	Ala.	Miss.	La.	Ark.	Tenn.	N.C.	S.C.
barberi	*	*	*	*	*	*	*	*	*
albimanus	*								
atropos	*		*	*	*			*	*
bradleyi	*	*	*	*	*				*
crucians	*	*	*	*	*	*	*	*	*
georgianus	*	*	*	*	*			*	*
pseudopunctipennis				*	*	*	*		
punctipennis	*	*	*	*	*	*	*	*	*
quadrimaculatus	*	*	*	*	*	*	*	*	*
walkeri	*	*		*	*	*	*		

EXPLANATION OF FIGURES

Figs. 1-60: All figures have been outlined with the aid of an ocular grid. Most of the illustrations were made from specimens somewhat flattened under a cover slip.



Anopheles albimanus Wied.

Fig. 1. Sidepiece. (setae, spicules, and scales not indicated). AS=accessory spines; IS=internal spine; PS=parabasal spine.

Fig. 2. Ninth tergite (NT) and anal lobe (AL). W=wrinkle in the anal lobe.

Fig. 3. Mesosome.

[2] Taken from King, Roth, Toffaleti, Middlekauf (1943).

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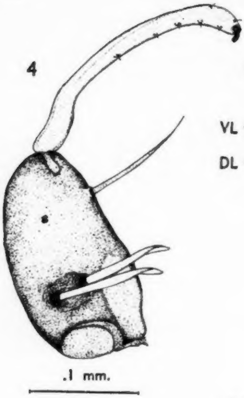

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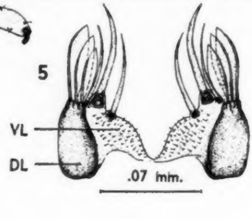

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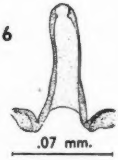

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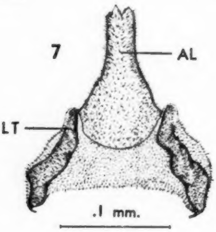

Anopheles barberi Coq.

Fig. 4. Sidepiece. (setae and spicules not indicated).

Fig. 5. Claspette.

DL=dorsal lobe; VL=ventral lobe.

Fig. 6. Mesosome.

Fig. 7. Ninth tergite and anal lobe (AL).

LT=lobe of ninth tergite.

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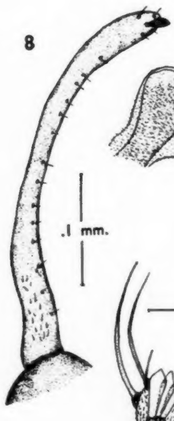

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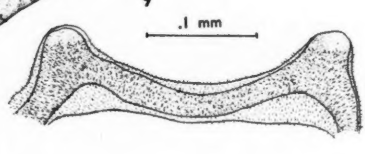

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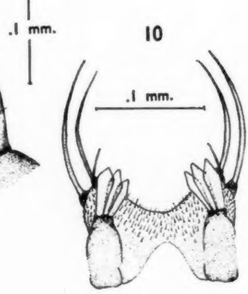

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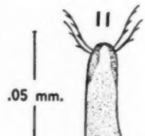
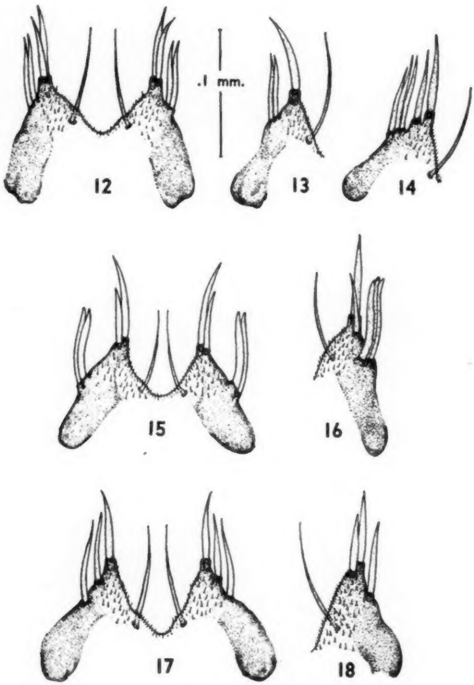


Anopheles pseudopunctipennis Theob.

Fig. 8. Clasper.
Fig. 9. Ninth tergite.
Fig. 10. Claspette.
Fig. 11. Mesosome.

and the differences in the male terminalia described by King (1939) will be used in the key.

The great similarity between males of anophelines with dark scaled wings makes the study of their genitalia often necessary before a positive identification can be made. With the increasing use of light traps for the collection of mosquitoes, the examination of male genitalia is frequently the only means of identifying specimens whose distinguishing color markings have been completely destroyed.



Anopheles crucians Wied., *Anopheles georgianus* King, *Anopheles bradleyi* King

Fig. 12. Claspette of *Anopheles crucians*.

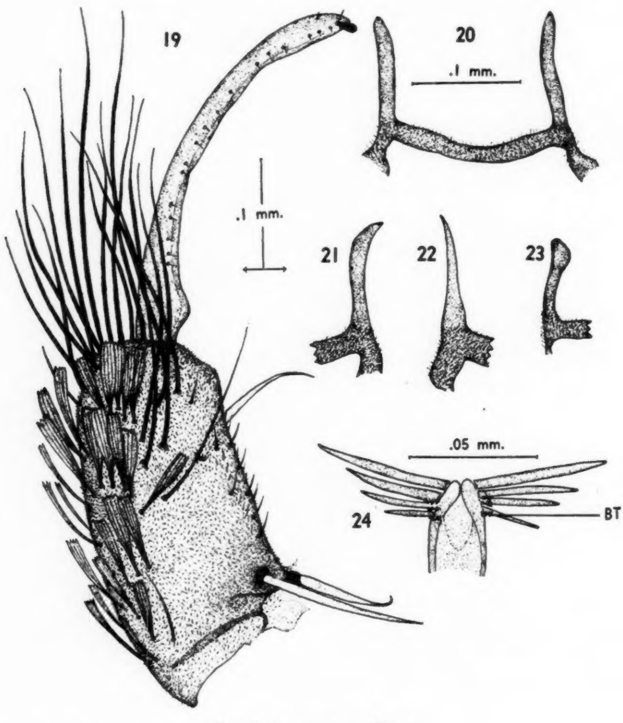
Figs. 13-14. Single lobes showing some of the variations which may occur in *Anopheles crucians*.

Figs. 15-16. Claspette and a single lobe showing a variation which may occur in *Anopheles georgianus*.

Figs. 17-18. Claspette and a single lobe showing a variation which may occur in *Anopheles bradleyi*.

(King, 1939 states that the claspettes of the type shown in Figs. 12, 15, and 17, are of average specimens).

The technique used in studying the genitalia is a simple one. Komp (1942) has described a method involving staining, dehydration and clearing for preparing genitalia for study. However, the present writer has found that clearing the genitalia in KOH is sufficient preparation for the study of our Southeastern species since most of their distinguishing characters are somewhat pigmented and therefore do not require staining. The use of a mounting medium, other than balsam, eliminates the necessity of dehydrating and clearing the specimen. The last two or three segments of the abdomen should be clipped off with a fine pointed scissors and transferred to 10% KOH. This is then heated for three to five minutes, care being taken to prevent boiling. With the aid of a pipette the specimen is then transferred to distilled water



Anopheles crucians Wied.

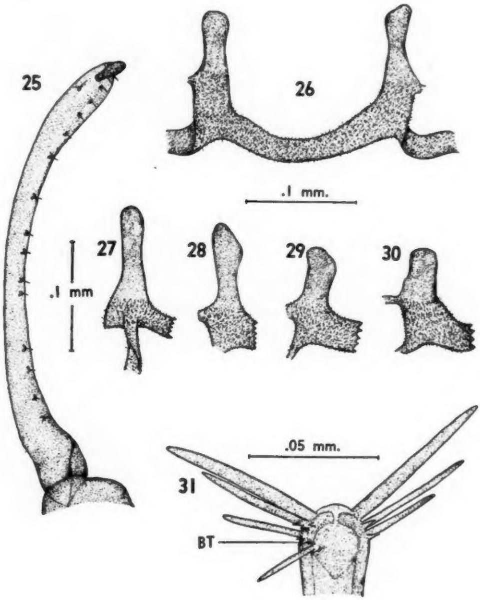
Fig. 19. Sidepiece.

Fig. 20. Pigmented band and lobes of the ninth tergite.

Figs. 21-23. Variations in the lobes of the ninth tergite.

Fig. 24. Apical portion of the mesosome showing the leaflets. BT=basal teeth.

and rinsed. Heating the water will help remove unnecessary tissue and the chitinous structures remain undissolved. The specimen is then placed in a drop of water or glycerine on a slide, and dissected with a pair of *minuten nadeln* at the end of applicators or match sticks. It is best to use the high power of a binocular dissecting microscope for this procedure. If a permanent mount is desired, the dissection may be made in a drop of chloral gum[3] and



Anopheles quadrimaculatus Say

Fig. 25. Clasper.
Fig. 26. Pigmented band and lobes of the ninth tergite.
Figs. 27-30. Variations in the lobes of the ninth tergite.
Fig. 31. Apical portion of the mesosome showing the leaflets.
BT=basal teeth.

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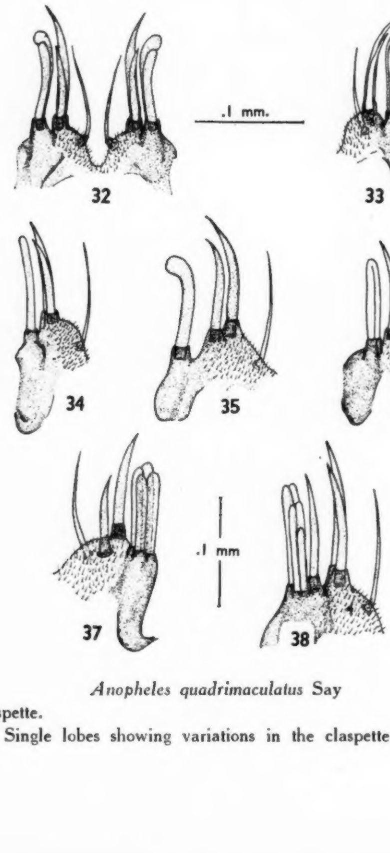
3 A formula for chloral gum is as follows:

gum arabic (clear lumps or powdered)	8 gms.
distilled water	8 cc.
glycerine	5 cc.
chloral hydrate	70 gms.
glacial Acetic Acid	3 cc.

(From King, Bradley, McNeel, 1942).

the specimen covered with a cover slip. It is important that the anal lobe, which is the hood-like structure arising from the ninth tergite, be removed because this membrane obscures the underlying structures that are used in determination of species. Removing the ninth segment usually brings with it the attached anal lobe and these should be mounted on the same slide with the other structures. Sometimes it may be desirable to dissect away the claspette lobes. Most of the drawings in this paper were made from structures which had been dissected and mounted individually. The characters in the key are those which can be seen clearly under the low and high powers of the compound microscope. However, oil immersion was used to check the presence of the basal teeth on the mesosomal leaflets in *A. quadrimaculatus, A. crucians* and *A. punctipennis* (Say). These structures are sometimes too small to be seen clearly under the high dry objective.

The following description of the genitalia (Fig. A) is more or less typical for the subgenus *Anopheles*. Specie differences are described in the key and



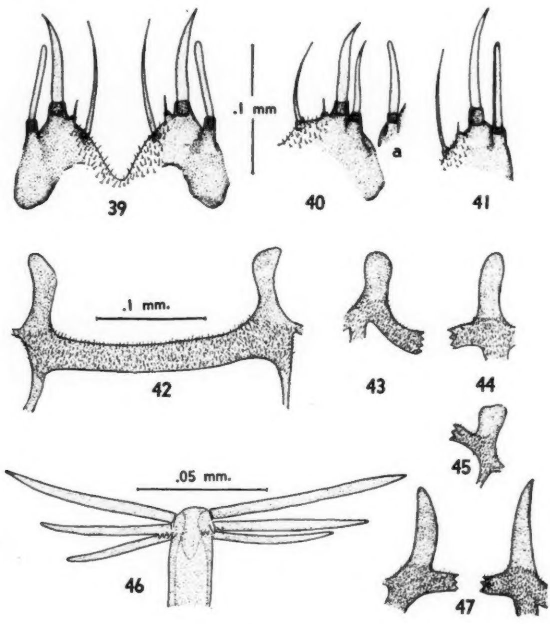
Anopheles quadrimaculatus Say

Fig. 32. Claspette.

Figs. 33-38. Single lobes showing variations in the claspette spines.

most of the characters are illustrated. Figure A is drawn from the dorsal position. Shortly after emergence the male terminalia (which include the abdominal segments caudad of the seventh; Freeborn, 1926) rotate 180 degrees so that the tergites are actually on the ventral side of the abdomen. If the specimen is mounted with the claspers up, the tergites are turned upwards and are then in their original morphological position. This is referred to as the dorsal side.

The genitalia begin with the ninth segment which forms a complete membranous ring. In most of our species, the tergite of this segment is a spicular membrane (MT) with a darkly pigmented supporting band (NT). Two smooth processes or lobes (LN) usually extend posteriorly (toward the claspers) from the opposite sides of this band. The dark band of the ninth tergite extends ventrally and broadens into a sternite band. The anal lobe (AL), attached to the inside border of the ninth tergite, is a high, somewhat



Anopheles punctipennis (Say)

Fig. 39. Claspette.

Figs. 40, 41. Single claspette lobes showing variations in the dorsal spines.

Fig. 40a. Another variation in the dorsal (outer) spine of claspette.

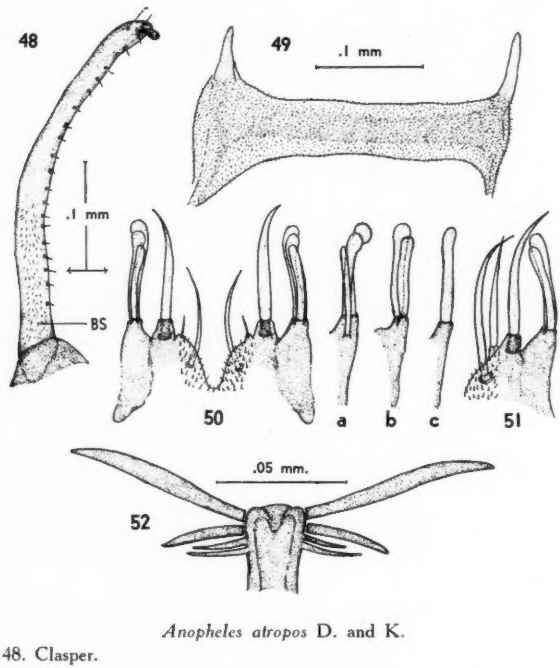
Fig. 42. Pigmented band and lobes of the ninth tergite.

Figs. 43-45, 47. Variations in the lobes of the ninth tergite.

Fig. 46. Apical half of the mesosome showing the leaflets.

triangular, pilose, membrane which lies over and covers the mesosome and claspette. This membrane is supported ventrally by the tenth sternites which, in some species, are distinct dark chitinous strips along the outer margins of the lobe (See Fig. 2).

The sidepiece (S) is fairly stout and slightly concave on the inner surface, spicular and setose, and sometimes bears scales (See Fig. 19). A long, slender, flattened, curved, clasper (C), bearing a small darkly pigmented terminal spine (T), is articulated from near the apex of the sidepiece. A row of small setae arising from distinct papillae, is usually found along the ventral surface of the clasper near its inner margin. The sidepiece lacks the distinct lobes which occur in *Culex* and *Aedes* but bears several large, stout spines which arise from prominent tubercles. A pair of parabasal spines (PS) are



Anopheles atropos D. and K.

Fig. 48. Clasper.

BS=basal hairs.

Fig. 49. Ninth tergite showing the lightly pigmented band and lobes.

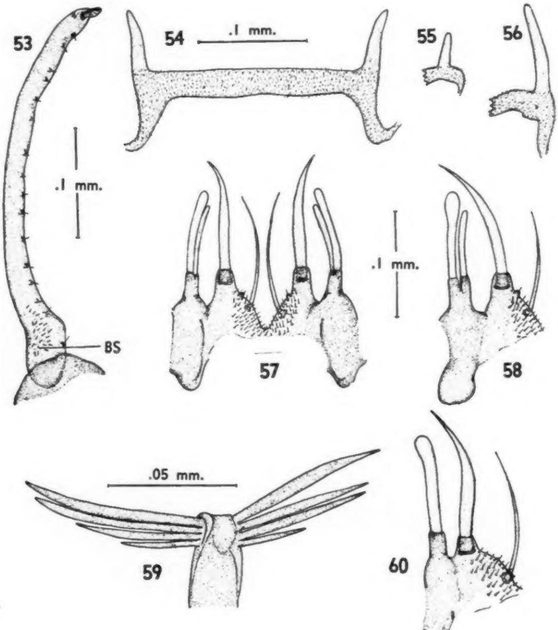
Fig. 50. Claspette.

Figs. 50, a, b, c. Variations in the dorsal spines of the claspette.

Fig. 51. A single claspette lobe showing a variation in the ventral spine of the claspette.

Fig. 52. Apical portion of the mesosome showing the leaflets.

found near the base, and these often arise from a slight elevation of the sidepiece which has been called elsewhere, the parabasal lobe. A single, more slender internal spine (IS) arises at about the middle of the inner margin of the sidepiece. Attached to the inner basal surface of the sidepiece is the paired, membranous claspette. This structure is often bilobed, forming a dorsal (D) and a ventral (V) lobe. Normally, the dorsal lobe lies directly above the ventral one and the dorsal spines often partly obscure the ventral spines. However, when under pressure of a cover slip, these lobes are usually flattened so that the different spines can be seen clearly. Since these two lobes are sometimes indistinct or fused, depending upon species or mounting, the outer

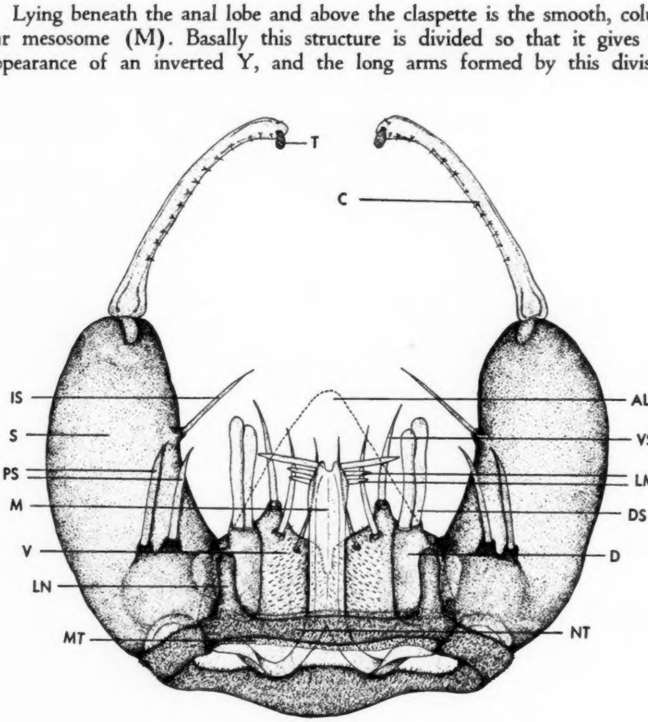


Anopheles walkeri Theob.

Fig. 53. Clasper.
BS=basal hairs.
Fig. 54. Pigmented band and lobes of the ninth tergite.
Figs. 55-56. Variations in the lobes of the ninth tergite.
Fig. 57. Claspette.
Figs. 58, 60. Single claspette lobes showing variations in the dorsal spines.
Fig. 59. Apical portion of the mesosome showing the leaflets.

portion of the claspette (nearest the sidepiece) is considered the dorsal or outer lobe, while the inner portion (nearest the median line) is the ventral or inner lobe. These lobes bear several spines. The ventral (inner lobe) is often partly spicular-pilose and somewhat lightly pigmented. It bears pointed apical spines (VS) and usually a more slender spine arising ventrally. The dorsal (outer lobe) is smooth, usually darkly pigmented, and often bears apically rounded (DS) or flattened spines.

Lying beneath the anal lobe and above the claspette is the smooth, columnar mesosome (M). Basally this structure is divided so that it gives the appearance of an inverted Y, and the long arms formed by this division



A

Fig. A. Semi-diagrammatic drawing of *Anopheles* genitalia (Dorsal View). AL=anal lobe (dotted line indicates the margin of the lobe); C=clasper; D=dorsal (outer) lobe of the claspette; DS=dorsal (outer) spines of the claspette; IS=internal spine of the sidepiece; LM=mesosomal leaflets (flattened); LN=lobes (processes) of the ninth tergite; M=mesosome; MT=membranous, spicular portion of the ninth tergite; NT=pigmented band of the ninth tergite; PS=parabasal spines of the sidepiece; S=sidepiece (setae and spicules have not been indicated); T=terminal spine of the clasper; V=ventral (inner) lobe of the claspette; VS=ventral (inner) apical spine of the claspette.

attach the mesosome to the base of each sidepiece. Several pairs of leaflets (LM) may be found at or near the apex of the mesosome. These are smooth, serrated, or toothed basally. The leaflets normally lie with their tips pointing upwards (toward the apex of the anal lobe), but when under pressure of a coverslip are flattened so that they may extend at about right angles to the mesosome. The apex of the mesosome is also usually curved upwards in a dorsal direction but when under pressure, it too becomes flattened and appears straight. In order to obtain a clear picture of the structures as they appear normally, it is best to examine the genitalia in water, glycerine, or chloral gum (without a cover slip), under the high power of a binocular dissecting microscope.

Examination of a large number of genitalia of our more common anophelines (*A. quadrimaculatus, A. punctipennis, A. crucians*) shows that much variation may occur in some of the structures used in determination of species. Not only may differences occur in different specimens of one species, but variations may be found in the paired structures of the same specimen. One specimen of *A. punctipennis* was found with three parabasal spines on one side (two on the other), and another genitalia lacked the dorsal lobe of the claspette on one side (present on the other), indicating that even the more constant characters are occasionally subject to variation. These variations undoubtedly explain the discrepancies in the description of anopheline genitalia in the literature. Table 2 shows the frequency with which variations occur in the spines of the claspette and lobes of the ninth tergite of *A. punctipennis* from different states in the southeast. It is interesting to note that not only the number but the shape of the spines on the dorsal lobes of the claspette may differ in certain individuals. The spines of *A. quadrimaculatus* (Table 3) vary mainly in number. This was also found to be the case with *A. crucians*. It should be kept in mind that not all specimens will conform to every character in the key. Many of the anopheline keys (and often descriptions of individual species) now found in the literature give only a few characters for differentiating the species and usually fail to consider the variations which are bound to occur. In this paper an attempt has been made to describe and illustrate some of the variations in the genitalia of our common anophelines.

The writer wishes to thank Lt. Col. W. V. King, Dr. Robert Matheson and J. L. Robertson, Jr., for use of some of their specimen material.

KEY TO THE SPECIES OF SOUTHEASTERN ANOPHELES BY MALE GENITALIA

1. Sidepiece with two large parabasal spines and one slender internal spine (Figs. 4, 19); anal lobe pilose (Fig. 7) ....Subgenus *Anopheles*.... 2

   Sidepiece with only one parabasal spine, one internal spine, and a pair of accessory spines (Fig. 1); anal lobe wrinkled but smooth (except for a small basal hairy region; Fig. 2); ninth tergite without lobes, the outer corners rounded and darkly pigmented, the central portion membranous, spicular, and lacking a pigmented band (Fig. 2); mesosome without leaflets (Fig. 3) ....Subgenus *Nyssorhynchus*, *A. albimanus*

2. Mesosome with leaflets (Figs. 11, 24, 31, 46, 52, 59); ninth tergite with a central sclerotized portion, the lobes, if present, connected by a darkly or lightly pigmented band (Figs. 9, 20, 26, 42, 49, 54).. 3

TABLE 2.—Variations in the claspette spines and lobes of the ninth tergite in *Anopheles punctipennis*.

Dorsal lobe of the claspette bearing					Ventral lobe bearing apically	Ninth tergite lobes	
a single sharp-pointed spine. (Fig. 40)	a single, fairly stout spine tapering to a rounded point. (Fig. 40a)	a single slender and apically rounded spine, the sides parallel or sometimes gradually tapering. (Fig. 39)	two slender apically rounded spines the sides parallel or gradually tapering. (Fig. 41)	one stout pointed spine and one slender rounded spine.	a single stout pointed spine and a minute spine arising from a large tubercle. (Figs. 39, 40, 41)	stout with the apex expanded or obliquely or roundly truncate. (Figs. 42-45)	stout with the sides tapering to a round or sharp point. (Fig. 47)
10*	1 (1)**	14 (7)	4 (6)	(1)	38	30 (2)	4 (2)

TABLE 3.—Variations in the claspette spines of *Anopheles quadrimaculatus*.

Dorsal lobe of claspette bearing					Ventral lobe of claspette bearing apically		
a single rounded spine. (Figs. 34, 35)	two rounded spines often partially fused. (Figs. 32, 36)	three rounded spines, sometimes two or all partially fused. (Fig. 33)	four rounded spines, some or all partially fused. (Fig. 37)	five rounded spines. (Fig. 38)	one pointed spine. (Fig. 36)	two pointed spines, one smaller than the other; sometimes a minute spine from a large tubercle may be present. (Figs. 32-35, 37)	three pointed spines. (Fig. 38)
1* (1)**	20 (8)	24 (9)	2 (1)	(1)	(6)	47 (8)	(3)

* The numeral indicates the number of specimens examined and found to possess that type of structure. These were bilaterally symmetrical.

** The numeral in parentheses shows the number of specimens with that type of structure but these were present on one side only, the other half being asymmetrical.

Mesosome without leaflets (Fig. 6); ninth tergite with the central portion lacking a sclerotized strip, the lobes not connected by a pigmented band (Fig. 7; rarely with an incomplete band); dorsal lobe of the claspette dark, somewhat oval, and bearing broad, flattened, apically curved and tapering filaments, the dorsal margin of each filament thickened (Fig. 5); ventral lobe with slender and stout spines (Fig. 5); sidepiece short and stout (Fig. 4); a very small species .... *A. barberi*

3. Mesosomal leaflets stout, smooth, or basally toothed (Figs. 24, 31, 46, 52, 59); ninth tergite with distinctly notable lobes (Figs. 20-23, 26-30, 42-45, 47, 49, 54-56) 4

Mesosomal leaflets very small, delicate and serrated (Fig. 11; these serrations are often difficult to see under the high dry objective); ninth tergite without distinct lobes, the processes represented by slight rounded elevations (Fig. 9); dorsal lobe of the claspette with flattened, broad tapering filaments (Fig. 10); ventral lobe dome-shaped, usually with two long incurving setae and a smaller seta between them (Fig. 10); clasper often with small hairs near the basal region (Fig. 8; see footnote No. 4) .... *A. pseudopunctipennis*

4. Claspette consisting of two triangular shaped lobes, the dorsal and ventral lobes of each indistinct; outer spines usually all acute (Figs. 12-18); sidepiece with scales, usually numerous (Fig. 19); lobes of ninth tergite very long, slender, and apically pointed or rounded (Figs. 20-22), rarely expanded (Fig. 23); one or more of the mesosomal leaflets with one or more coarse or fine basal teeth (Fig. 24) 5

Claspette not consisting of two triangular shaped lobes, the dorsal and ventral lobes of each usually more or less distinct; outer spines rounded or sometimes pointed (Figs. 32-38, 39-41, 50, 50a, b, c, 51, 57, 58, 60); sidepiece with very few, or lacking, scales; lobes of ninth tergite usually not as above (Figs. 26-30, 42-45, 49, 54-56) 6

5. Claspette lobe usually with three, four, or five apical and external spines, which may be flattened, or slender and tapered (Figs. 12-18) .... *A. crucians*, *A. georgianus*, *A. bradleyi*

The claspette spines of *A. georgianus* and *A. bradleyi* are somewhat distinctive and may be separated by the following characters:

Claspette lobe with two stout, sharp pointed, closely set, apical spines, the outer shorter than the inner; a second pair of flattened, somewhat blade-shaped, closely set spines, of about equal length on the outer margin (Fig. 15); occasionally only one or three external spines on each lobe (Fig. 16) .... *A. georgianus*

Claspette lobe usually with three apical and external spines which may be about equally spaced (Fig. 17) or two of them closely set at the apex (Fig. 18); occasionally only two or four spines on one or both sides .... *A. bradleyi*

King (1939) states that as a result of variations, the genitalia of individual specimens of *A. crucians* may resemble either *A. bradleyi* or *A. georgianus*. Figs. 12-14 show some of the variations in the claspette spines of *A. crucians*. Other modifications in the arrangement of these spines may also occur.

6. Lobes of the ninth tergite stout, the apex expanded or obliquely or roundly truncate (Figs. 26-30, 42-45), rarely tapering to a round or pointed tip (Fig. 47); minute hairs [4] on the basal portion of the clasper usually lacking (Fig. 25; these hairs may appear spicular in some mounts; they should not be confused with the row of small setae arising from somewhat distinct papillae or tubercles; most of these setae are arranged along the inner margin of the clasper); one or more of the mesosomal leaflets with one or more coarse or fine basal teeth (Figs. 31, 46); the lobes and band of the ninth tergite darkly pigmented 7

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[4] Root (1923) noted these structures on the claspers of *A. walkeri* and *A. atropos* and called them non-papillated hairs. They are similar to the non-papillated hairs (Aitken) found on the claspers of *A. occidentalis* D. and K. and *A. freeborni* Aitken mentioned by King and Bradley (1941) in their key to the Nearctic anophelines.

Lobes of the ninth tergite slender, tapering, with a slightly rounded or pointed tip (Figs. 49, 54-56); basal region of the clasper with minute hairs 4 ("non-papillated hairs"; Figs. 48, 53); mesosomal leaflets smooth (Figs. 52, 59); lobes and band of the ninth tergite sometimes comparatively lightly pigmented...... 8

7. Dorsal (outer) spines of the claspette usually two or three in number (Figs. 32, 33, 36) sometimes one, four or five (Figs. 34, 35, 37, 38), stout, rounded, the sides parallel, sometimes partially fused or expanded at the tip; at least one or a fused pair of the outer spines as wide as or wider than the apical spine of the ventral lobe; the outer spine is rarely more slender than the apical spine of the ventral lobe (Fig. 34); ventral lobe of the claspette usually with two sharp pointed apical spines (Figs. 32-35, 37), rarely with one or three apical spines, (Figs. 36, 38) and sometimes a minute spine from a large tubercle; a comparatively slender spine arises ventrally on the inner lobe; (See Table 3 for the frequency of variations in the claspette spines); spicules or hairs on the ventral lobe are generally present on the region below the large apical spines; sidepiece without scales .... *A. quadrimaculatus*

Dorsal (outer) spine (or spines) usually slender, apically rounded (Figs. 39, 40a, 41) or pointed (Fig. 40) with parallel or tapering sides (the outer spine is generally much more slender than the apical spine of the ventral lobe); if the outer spine is somewhat stout it may taper to a round or sharp point (Fig. 40a); ventral lobe with one large sharp pointed apical spine, a minute spine arising from a large tubercle, and a slender one arising ventrally; the hairs on the ventral lobe of the claspette are usually restricted to the inner portion with very few, if any, on the region below the apical spine (Figs. 39, 40, 41); (See Table 2 for the frequency of the variations in the claspette spines); sidepiece usually with a few scales.. *A. punctipennis*

8. Mesosomal leaflets with the second pair from the apex (at least on one side) less than half the length of the first pair (Fig. 52); basal hairs on the clasper fairly numerous, the area covered often extending one third or one half the length of the clasper (Fig. 48) .... *A. atropos*

Mesosomal leaflets with the second pair from the apex usually more than half the length of the first pair (Fig. 59); basal hairs on the clasper usually few in number and often restricted to a small basal region (Fig. 53) .... *A. walkeri*

(The claspettes of *A. atropos* and *A. walkeri* are very similar. Compare Figs. 50-51 and 57, 58, 60).

REFERENCES

FREEBORN, STANLEY B. 1926—The Mosquitoes of California. University of California Publication, Technical Bulletins, Vol. 3.

KING, W. V. 1939—Varieties of *Anopheles crucians* Wied. Amer. Journal Trop. Med. **19**:461-471.

KING, W. V. AND G. H. BRADLEY. 1941—General Morphology of *Anopheles* and Classification of the Nearctic Species. *In* Human Malaria, Amer. Assoc. Adv. Sci. Pub. **15**:63-70.

KING, W. V., G. H. BRADLEY, AND T. E. MCNEEL. 1942—The Mosquitoes of the Southeastern United States. Misc. Pub. **336** (Revised) U. S. D. A.

KING, W. V., L. M. ROTH, J. TOFFALETTI, AND W. W. MIDDLEKAUFF. 1943—New Distribution Records for the Mosquitoes of the Southeastern United States During 1942. Jour. Eco. Entom. **36**:573-577.

KOMP, W. H. W. 1942—A Technique for Staining, Dissecting, and Mounting The Male Terminalia of Mosquitoes. Public Health Reports **57**:1327-1333.

ROOT, F. M. 1923—The Male Genitalia of some American *Anopheles* Mosquitoes. Amer. Jour. of Hygiene **3**:264-279.

SIMMONS, J. S. AND T. H. AITKEN. 1942—The Anopheline Mosquitoes of the Northern Half of the Western Hemisphere and of the Philippine Islands. Army Med. Bull. **59**.

BROOKLEY FIELD, ALA.

The Crayfishes of Kentucky, with Notes on Variation, Distribution and Descriptions of New Species and Subspecies

Rendell Rhoades

Introduction

This study was undertaken in order to close a gap which has long existed in our knowledge of the distribution of the crayfishes. The Crustacea of the majority of the surrounding states have been studied and, in many cases, problems have arisen the solutions of which lie within this territory. Until the work of Ortmann (1931) our knowledge of the Kentucky crayfishes was too fragmentary to formulate distribution for any species. A few classical records of fourteen species had been repeated through nearly a century of literature.

During the course of this study each of the one hundred and twenty counties has been visited. The samples are, for the most part, quantitative. The detailed work necessary for the quantitative analysis of the state's crustaceans is beyond the scope of this paper. It is my desire that this preliminary study encourage others to add to these remarks concerning the crayfishes of the Commonwealth of Kentucky.

The commercialization of many species of our wildlife, including the crayfishes, and the accompanying drastic change in the condition of the land may have suppressed or enlarged the former distribution of many species. The rivers and lakes of a century ago were clearer and colder and the sweet water table was closer to the surface. No doubt, the *Cambarus (s. s.)* exceeded at least quantitatively, the present population. The *Procambarus* and *Orconectes* are probably produced in greater numbers today in the warm muddy waters. Decrease in predators may account, to a considerable extent, for the increase in the crayfishes, according to Dr. Edwin P. Creaser. Unfortunately, old records are too scarce or not available for verification so that we must content ourselves with the study of the present condition of these faunal units.

The importance of the crayfish in relation to other aquatic organisms is well illustrated by a situation existing in south central Kentucky. Northward the black bass hatch late in May and early in June. The crayfishes, *Orconectes propinquus sanborni* and *Orconectes rusticus rusticus*, rear their young in late April and early May. Thus, the young crayfishes are too large to be utilized to the fullest extent by the small bass. The crayfish diet can not start until the hatch of the second year is available. The *Orconectes juvenilis* of central and southern Kentucky rear their young late in May and early in June when the young bass are from one to one and one-half inches long. Stomachs of the Smallmouthed Bass, *Micropterus dolomieu dolomieu* Lacé-

pède, and the Kentucky Bass, *Micropterus punctulatus punctulatus* (Rafinesque), are often packed with crayfishes less than ten millimeters in length during this time of the year.

ACKNOWLEDGEMENTS

There are many who have contributed to the work presented here. I take this opportunity to express my gratitude for the continued assistance of Dr. Waldo L. Schmitt, Curator, Division of Marine Invertebrates, United States National Museum. Dr. Fenner A. Chace, Jr., Assistant Curator of Marine Invertebrates, Museum of Comparative Zoology, Harvard College, has rendered invaluable service in making available to me the Kentucky records of his museum. The Kentucky material in the collections of the Museum of Zoology of the University of Michigan was placed at my disposal by Dr. Karl E. Goellner, Division of Crustacea. Continued communications with Dr. G. Ayres Coventry, Research Associate, Academy of Natural Sciences of Philadelphia, especially in regards to *Orconectes pellucidus pellucidus*, has been most helpful during this study. Mr. R. Taylor Hoskins, Superintendent, Mammoth Cave National Park, and his staff have generously assisted me in securing specimens from the park area and have provided me with information on the occurrence of the blind crayfish. The records from Mammoth Onyx Cave and Hidden River Cave were secured through the kindness of Dr. E. R. Pohl, manager and naturalist. I wish to express my thanks to the Kentucky Division of Game and Fish for cooperation in conducting the field work necessary for this paper. Dr. Raymond C. Osburn, Chairman, Department of Zoology and Entomology, Ohio State University, deserves an expression of gratitude for valuable suggestions on this problem. It has been my good fortune to have the very gracious cooperation of Mrs. Ethel M. Miller, Botany and Zoology Librarian, Ohio State University. Miss Florence A. Hellman, Chief Bibliographer, Library of Congress, has been of much assistance in clarifying matters relative to Dr. Th. G. Tellkampf and his obscure work on the animals of the Mammoth Cave. Dr. Frank O. Hazard, Head of the Biology Department, Wilmington College, who has been my professor and associate, is worthy of mention for the many courtesies rendered by his department and Wilmington College. There is one who has patiently shared the weariness of many long days of collecting under the most strenuous conditions and who, though the study became ever more engrossing, never failed to encourage and assist. For the sacrifices so graciously made I award this special expression of appreciation to my wife—Evelyn Baxter Rhoades.

Historical

The first species of crayfish reported from Kentucky was "*Astacus pellucidus,*" referred to as "*Astacus bartoni*(?)," from the Mammoth Cave and presented to the Academy of Natural Sciences of Philadelphia at the meeting of May 24, 1842. Tellkampf (1844:383) described and named the species. Girard (1852:88) described "*Cambarus rusticus*" from, "The Ohio, at Cincinnati.", properly a Kentucky record. Hagen (1870:66 67) described "*Cambarus juvenilis*" from Mr. Alphaeus Hyatt's specimens from, "Little Hickman, Kentucky River." *Cambarus bartoni* was recorded from two localities in the state (Hagen, 1870:79-80). Bundy believed that "*Cambarus sloani*" would be found in, "Northern Kentucky" (1876:24). Faxon described *Cambarus cornutus* (1884:120), "*Cambarus propinquus sanborni*" (1884:129), and "*Cambarus putnami*" (1884:132) from Kentucky and also included the first record from the state for *Cambarus diogenes* (1884:144). *Cambarus bartoni tenebrosus* was described from the Mammoth Cave by Hay (1902:301). He also reported "*Cambarus propinquus*" from the Green River but admits that the identification is questionable. *Cambarus extraneus* was first collected in

Kentucky by Mr. E. B. Williamson (Ortmann, in: Williamson, 1905:310-311). Shull (1909:301) refers to a *Cambarus bartoni* similar to the Indiana form, which is probably *Cambarus bartoni laevis*, from Fayette county. "*Cambarus graysoni*" was described from Grayson Springs by Faxon (1914:393). Ortmann (1931:76-77) added one more species, "*Cambarus (Faxonius) rusticus placidus*," to the Kentucky list to bring the total to fifteen species.

The present paper includes twenty-seven species and subspecies for the state. The previous list of fifteen has been reduced to eleven by synonymy and removal of doubtful records. Six species by former authors are added as well as ten new species and subspecies here described.

Systematic List of Kentucky Crayfishes

Family ASTACIDAE

Subfamily Cambarinae

Genus PROCAMBARUS Ortmann (1905)

1. *Procambarus clarki* (Girard) 1852.
2. *Procambarus blandingi acutus* (Girard) (1852).

Genus ORCONECTES Cope (1872)

Section LIMOSUS Ortmann (1931)

Group RAFINESQUEI

3. *Orconectes rafinesquei* n. sp.
4. *Orconectes tricuspis* n. sp.
5. *Orconectes pellucidus pellucidus* (Tellkampf) (1844).
6. *Orconectes pellucidus packardi* n. ssp.
7. *Orconectes kentuckiensis* n. sp.

Section PROPINQUUS Ortmann (1931)

Group PROPINQUUS Ortmann (1931)

8. *Orconectes propinquus jeffersoni* n. ssp.
9. *Orconectes propinquus sanborni* (Faxon) (1884).

Group RUSTICUS Ortmann (1931)

10. *Orconectes rusticus barrenensis* n. ssp.
11. *Orconectes rusticus placidus* (Hagen) (1870).
12. *Orconectes rusticus rusticus* (Girard) (1852).
13. *Orconectes juvenilis* (Hagen) (1870).
14. *Orconectes bisectus* n. sp.

Section VIRILIS Ortmann (1931)

Group VIRILIS Ortmann (1931)

15. *Orconectes immunis immunis* (Hagen) (1870).

Group COMPRESSUS Ortmann (1931)

16. *Orconectes compressus* (Faxon) (1884).

Genus CAMBARUS Erichson (1846)

Section EXTRANEUS Ortmann (1931)

17. *Cambarus rusticiformis* n. sp.
18. *Cambarus cornutus* Faxon (1884).
19. *Cambarus extraneus* Hagen (1870).

Section BARTONI Ortmann (1931)

20. *Cambarus distans* n. sp.
21. *Cambarus bartoni bartoni* (Fabricius) (1798).
22. *Cambarus bartoni striatus* (Hay) (1902).
23. *Cambarus bartoni laevis* Faxon (1914).
24. *Cambarus bartoni tenebrosus* Hay (1902).
25. *Cambarus bartoni ornatus* n. ssp.
26. *Cambarus ortmanni* Williamson (1907).

Section DIOGENES Ortmann (1931).

27. *Cambarus diogenes* Girard (1852).

Discussion of Species

PROCAMBARUS CLARKI (Girard) (1852)

Distribution and Ecology.—This species, new to the list of crayfishes from the commonwealth, was found in one locality in Kentucky in company with *Procambarus blandingi acutus*. The habitat was a mud bottom slough with vegetation composed of many species which indicated considerable permanency of the waters. It may be expected in other lowland sloughs and bayous in Hickman and Fulton counties.

Taxonomic Remarks.—Hagen (1870:40) states that "There is rarely one spine at the side of the thorax." The adult female in my collection bears a low tubercle with an upright corneous tip and the small females have the lateral spines wanting. The antennal scale is broader in my specimens than in Hagen's and the tuberculation of Hagen's *C. clarkii* (Pl. 4) exceeds by far the armature of my Kentucky specimens. The hands are shorter and broader than *P. blandingi acutus* and specimens of more typical *clarki* from the south.

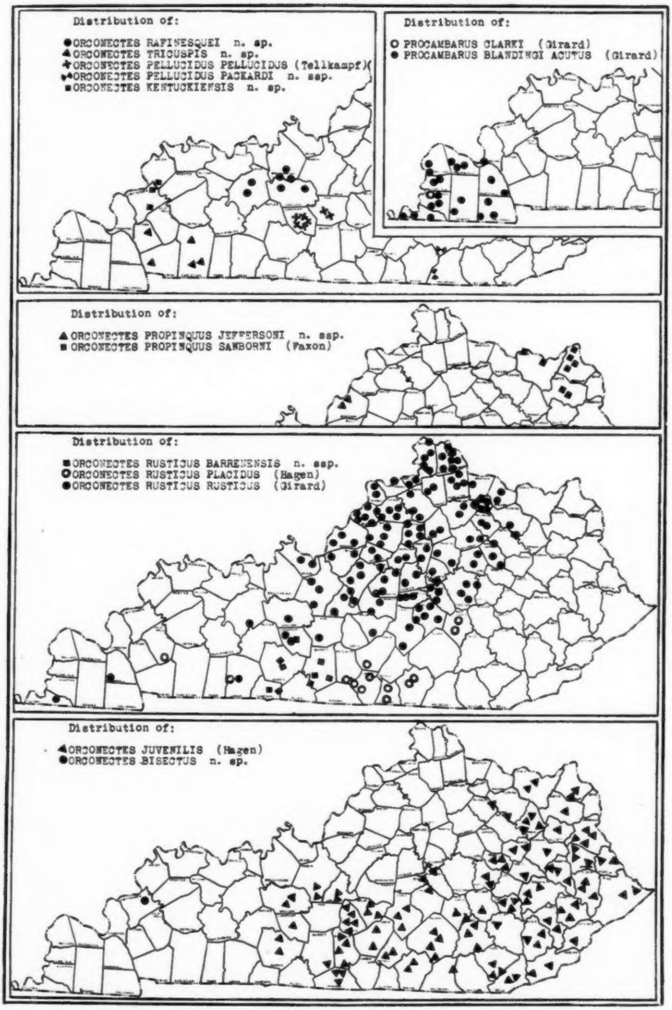
ORTMANNICUS BLANDINGI ACUTUS (Girard) (1852)

Distribution and Ecology.—In Kentucky the species was frequently encountered in the streams of the Jackson Purchase.* It must ascend the Ohio at least to the mouth of the Wabash as indicated by its presence in that drainage. The crayfish prefers lowland sand and gravel streams and muddy sloughs where cover requirements are usually furnished by submerged wood or growing vegetation. It occasionally occupies the burrows of *Orconectes immunis immunis* and *Cambarus diogenes*, but is usually not a burrower itself. The species is rather tolerant regarding ecological factors.

Taxonomic Remarks.—The lateral spines of the carapace are rarely absent.

* The counties of Kentucky between the Tennessee River and the Mississippi.

The marginal spines of the rostrum are very small or wanting. The tubercles of the annulus are usually rather high but specimens from western Kentucky occasionally have low tubercles on the annuli. This seems to be true even more in the immature females. I am not able to distinguish local races since the species is subject to great individual variation.



Orconectes rafinesquei n. sp.

Kentucky Records: OHIO RIVER SYSTEM—Rough River, Falls-of-Rough, Grayson-Breckenridge counties. (5 m I; 18 m II; 32 f September 3, 1941).—TYPE LOCALITY—North Fork of Rough River, 2 mi. nw. of McDaniels, Breckenridge County. (3 m II; 2 f May 13, 1941). Rough River, at Eveliegh, Breckenridge County. (1 m I; 4 m II; 2 f (1 with young) May 13, 1941). Big Clifty Creek, 1 mi. e. of West Clifty, Grayson County. (2 m I; 10 f September 3, 1941).

Distribution and Ecology.—Orconectes rafinesquei was found only in the Rough River and tributaries where it was the dominant species. It lives in streams under stones and other cover but will make shallow burrows if cover is absent and the stream bed is muddy. At the type locality my specimens were found under debris on a solid rock bottom.

Description—Male, form I.—Rostrum of moderate length, moderately excavated with straight, slightly converging sides. Marginal spines prominent and acute. Acumen moderately long, with concave sides and acute upturned tip. Cervical groove not sinuate but interrupted on the sides above acute lateral spines. Branchiostegal spines wanting. Areola rather short, varying from 28.5 to 33.5 per cent of the total length of the carapace, and rather narrow, rarely more than one-fifth as wide as long. Carapace cylindrical and uniformly covered with light granules.

Antennal scale oblong or obovate. Stout apical spine of moderate length which slightly exceeds the tip of the rostrum. Epistoma with free edges rounded and elevated except at the terminal tooth. Chelipeds rather stout. Chelae two to two and one-half times as long as broad. Movable finger nearly twice as long as the inner margin of the palm. Palm somewhat inflated and lightly punctate above. Inner margin marked by six or eight small depressed tubercles and as many or more in a secondary row. Inner margin of the movable finger also marked by similar tubercles. Fingers only slightly gaping at the base. Apposition edges of fingers bearing several denticles. Fingers costate and a beard is usually present at the inner base of the immovable finger. Carpus bearing one spine on the middle of the inner face. Meros bispinose anteriorly above. Inner terminal spine of the biserial row large and followed proximally by an inconspicuous row of spines. One spine on the middle of the anterior ventral margin. Hooks on the third walking legs stout and erect. Hooks of the fourth walking legs absent.

Gonopods short, reaching to, or slightly beyond, the coxopodites of the third walking legs, and with the tips split for only a short distance. The tip of the outer ramus corneous and barely longer than the inner. Appendage thickest at the middle.

Form II.—Hooks of the third walking legs represented by tubercles. Gonopods barely reaching the coxopodites of the second walking legs and of nearly uniform diameter throughout. Tips equal in length and fleshy and blunt.

Female.—Annulus ventralis oval and level with the thoracic sterna. Posterior border slightly raised. Surface marked by two low, widely spaced tubercles behind the anterior margin. Median furrow variable but usually beginning be-

hind the left tubercle and around the end of a slender projection as a wide sulcus. Posteriorly it narrows and bends once in a wide arc to the right and returns to the median line to proceed for a short distance in a straight line to the posterior margin.

Measurements of the type specimens are:—

	I	II	F
Total length	49.2 mm.	48.5 mm.	48.9 mm.
Length of carapace	23.9	23.3	23.0
Length of rostrum	6.1	7.1	6.5
Length of areola	8.1	7.6	7.2
Length of right cheliped	35.3	29.9	28.8
Length of right chela	18.5	15.0	13.2
Length of inner margin of palm	6.5	4.6	4.0
Length of movable finger	12.6	10.2	8.5
Length of abdomen	25.3	25.2	25.9
Width of carapace	12.6	11.5	11.4
Width of base of rostrum	3.1	3.2	3.5
Width of right chela	9.2	6.7	6.1
Width of 2nd abdominal segment	10.3	9.8	10.3

The type collection was taken from the Rough River, at Falls-of-Rough, Grayson-Breckenridge counties, Kentucky. The holotype, male, form I, is U.S.N.M., No. 81304; the allotype, male, form II, is U.S.N.M., No. 81305; and male, form II, the allotype, female, is U.S.N.M., No. 81306.

Paratypes from the same locality are deposited in the Museum of Comparative Zoology, the Academy of Natural Sciences of Philadelphia, the Museum of Zoology, University of Michigan, and the collection of the writer.

The species is named to honor the great naturalist of Transylvania — Constantine Samuel Rafinesque.

Affinities.—This species and the four species following belong to the "Section of *C. limosus.*" The gonopods are short and the tips are separated for only a short distance. However, the tips are both recurved in the same direction in *O. rafinesquei, O. tricuspis, O. pellucidus pellucidus, O. pellucidus testii* (Hay) (1893), *O. pellucidus australis* (Rhoades) (1941), *O. pellucidus packardi, O. kentuckiensis,* and *O. harrisoni* (Faxon) (1884). These species should compose a new, "Group rafinesquei." A second group under Ortmann's "Section of *C. limosus*" is composed of *O. limosus* (Rafinesque) (1817), *O. sloani* (Bundy) (1876), and *O. indianensis* (Hay) (1896) and may be designated as the "Group limosus." This second group is characterized by strongly diverging tips of the gonopods.

Orconectes tricuspis n. sp.

Kentucky Records:—OHIO RIVER SYSTEM—Cumberland River Drainage. Pilfer Creek, 2 mi. e. of Eddyville, Lyon County. (3 m II May 15, 1941). Pilfer Creek, 4 mi. e. of Eddyville, Lyon County. (1 m II May 15, 1941). "Little River, 4 mi. se. of Cadiz, Trigg County." (1 f). (M. M. Z.). "South Fork of Little River, 2 mi. s. of Hopkinsville, Christian County." (1 m I; 4 f June 6, 1932, Ameel and Hedrick, coll.). (M. M. Z.). South Fork of Little River, 4 mi. w. of Fairview, Christian County. (4 m II; 1 f May 14, 1941). Pete Light's Spring, 3 mi. e. of Canton, Trigg County.

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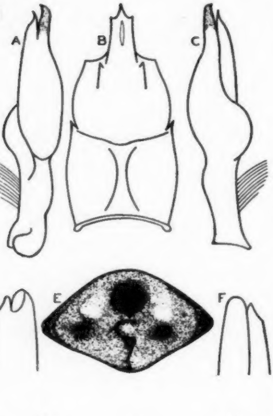

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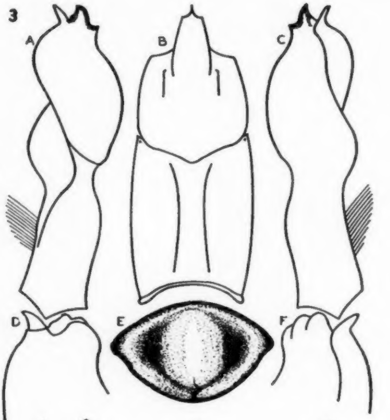

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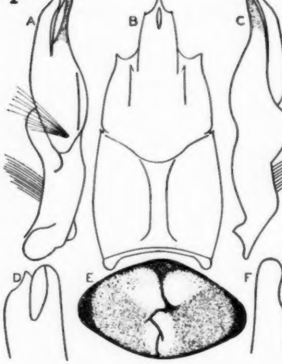

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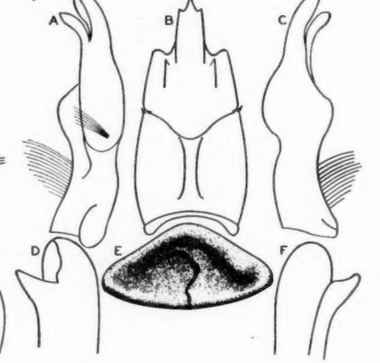


Fig. 1.—*Orconectes rafinesquei*, new species: A, Gonopod, male, form I, inner view; B, dorsal view of carapace; C, gonopod, male, form I, outer view; D, tip of gonopod, male, form II, inner view; E, annulus ventralis; F, tip of gonopod, male, form II, outer view.

Fig. 2.—*Orconectes tricuspis*, new species: A, Gonopod, male, form I, inner view; B, dorsal view of carapace; C, gonopod, male, form I, outer view; D, tip of gonopod, male, form II, inner view; E, annulus ventralis; F, tip of gonopod, male, form II, outer view.

Fig. 3.—*Orconectes pellucidus packardi*, new subspecies: A, Gonopod, male, form I, inner view; B, dorsal view of carapace; C, gonopod, male, form I, outer view; D, tip of gonopod, male, form II, inner view; E, annulus ventralis; F, tip of gonopod, male, form II, outer view.

Fig. 4.—*Orconectes kentuckiensis*, new species: A, Gonopod, male, form I, inner view; B, dorsal view of carapace; C, gonopod, male, form I, outer view; D, tip of gonopod, male, form II, inner view; E, annulus ventralis; F, tip of gonopod, male, form II, outer view.

(3 m I; 1 m II; 5 f September 4, 1941).—TYPE LOCALITY—Tradewater River Drainage. Head of Tradewater River, 4 mi. n. of Hopkinsville, Christian County. (2 m II; 3 f (1 with eggs) May 14, 1941).*

Distribution and Ecology.—The species is distributed in the Cumberland and upper Tradewater in western Kentucky and will probably be found to extend into Tennessee.

O. tricuspis was found in small gravelly upland streams under stones or any other large objects which might provide cover. At the type locality they had moved a considerable quantity of gravel from under a concrete wall to form roomy burrows.

Description—Male, form I.—Rostrum rather long, moderately excavated, sides straight and subparallel. Marginal spines acute. Acumen rather long and acute with concave sides. Prominent broad median carina. Cervical groove slightly sinuate and interrupted above a sharp lateral spine on each side. Areola greater than one-third of the total length of the carapace varying from 32.4 to 35.1 per cent. The width is from one-sixth to one-fifth of its own length. Carapace smooth and cylindrical.

Antennal scale small, rather narrow, and slightly obovate with a short apical spine. Free edges of the epistoma rounded, slightly elevated, and ending in a mucronate tip. Chelipeds rather slender, more so at least than the other members of the *limosus* section. Chelae flattened and keeled externally. Fingers costate and rarely gaping with the apposition edges marked by four to six denticles each. Inner margin of the palm marked by many squamose tubercles in two irregular rows. The base of the movable finger bears a few similar tubercles. Carpus bears a strong spine in the middle of the inner face, another in a central position ventrally, and one at the lateral anterior articulation with the hand. Meros bispinose anteriorly above. Ventrally, the inner series of spines well developed and the outer row represented only by a terminal spine. Hooks on the third walking legs blunt and somewhat depressed. Hooks of the fourth walking legs absent.

Gonopods short, split for a short distance, and without a shoulder. Rami somewhat incurved throughout their entire length. Tips also incurved and inner tip curved outwardly to lie laterally to the inner. Tips equal in length, or inner fleshy tip barely exceeding the outer corneous tip.

Male, form II.—Hooks on the third walking legs reduced to erect knobs. Rami in close contact for their full length and the tips only slightly separated. Inner ramus inflated to make the diameter uniform throughout the appendage. Tips equal in length or inner barely exceeding the outer.

Female.—Chelae shorter and stouter. Annulus ventralis oval with lateral extremities low. Middle of anterior wall sloping up gently to two high tubercles; the right forming a slight hook behind the left. The median furrow begins around this hook, forms another hook to the right, straightens and proceeds over a high posterior tubercle to the posterior wall.

* *C. propinquus* from Crofton, Christian Co. (Goodnight, 1940, Rept. Reelfoot Lake Biol. Sta., IV:170) is probably this species.

Measurements of the type specimens are:—

	I	II	F
Total length	59.8 mm.	58.9 mm.	50.5 mm.
Length of carapace	29.8	28.6	25.0
Length of rostrum	8.3	7.6	7.3
Length of areola	9.7	9.5	8.0
Length of right cheliped	42.2	41.1	28.2
Length of right chela	22.3	20.9	12.6
Length of inner margin of palm	7.3	6.9	4.6
Length of movable finger	15.2	13.1	8.0
Length of abdomen	30.6	30.3	25.5
Width of carapace	15.0	14.6	11.7
Width of base of rostrum	4.4	4.1	3.6
Width of areola	2.1	2.1	1.7
Width of right chela	9.1	8.3	6.3
Width of 2nd abdominal segment	12.5	12.3	11.4

Types have come from two localities. The holotype, male, form I, from Pete Light's Spring, 3 mi. e. of Canton, Trigg County, Kentucky, is U.S.-N.M., No. 81307; the allotype, male, form II, from Pilfer Creek, 2 mi. e. of Eddyville, Lyon County, Kentucky, is U.S.N.M., No. 81308; and the allotype, female, from Pete Light's Spring, 3 mi. e. of Canton, Trigg County, Kentucky, is U.S.N.M., No. 81309. Paratypes from the Trigg County locality are deposited in the Museum of Comparative Zoology and the collection of the writer. A paratype female from Little River, Trigg County, is in the collection of the Museum of Zoology, University of Michigan.

Affinities.—This species belongs to the "Section of *C. limosus*" though it has a higher annulus and a little thicker gonopod than other members. In specimens from Christian County the three tubercles are somewhat obliterated but the whole surface is strongly convex. This annulus and the thick stocky gonopods with the diminutive tips preclude the blind species of the Mammoth Cave. The rostrum of the Christian County specimens is longer and narrower and the margins straight.

ORCONECTES PELLUCIDUS PELLUCIDUS (Tellkampf) (1884)*

Distribution and Ecology.—*Orconectes pellucidus pellucidus* with its subspecies is distributed through an extensive subterranean stream system in the limestone region extending from southern Indiana to northern Alabama.

O. p. pellucidus was brought to the attention of science just a century ago. During the years subsequent workers on the cave animals have produced a maze of records from which mine have been chosen in order to have a complete set of localities without repetition of records. Old writers, no doubt, collected generally in the cave area but labelled the specimens as if coming from the Mammoth Cave. I am able to add two records from Hart County. The *O. p. pellucidus* of Mammoth Onyx Cave were introduced from Hidden River Cave. The Edmonson County records are mostly from the immediate vicinity of the Mammoth Cave.

* A record from the "New Discovery" Mammoth Cave has been furnished through the courtesy of Mr. Kenneth N. Dearolf, Educational Director, Dayton Public Library Museum, Dayton, Ohio, who has mentioned it in an unpublished manuscript on entomological work in the "New Discovery."

We may expect this crayfish in most of the underground streams of the limestone uplands of west central Kentucky from Bullitt, Meade, and Breckenridge counties of the Ohio to Allen, Simpson, and Logan counties on the Tennessee line.

Orconectes pellucidus packardi n. ssp.

Kentucky Records:—OHIO RIVER SYSTEM—Cumberland River Drainage. Cumberland Crystal Cave, at Alpine, Pulaski County. (U. S. N. M., No. 75821, 1 m II; 3 f G. M. Ehlers, coll.). (2 m I; 2 f October 7, 1941) (4 m I; 3 m II; 3 f January 27, 1942).—TYPE LOCALITY.

Distribution and Ecology.—This new subspecies is distributed in the limestone caverns of the upper Cumberland and South Fork. I observed a specimen in Eureka Cave, 6 mi. w. of Parkers Lake, McCreary County, but did not collect it since Mr. Perkins, one of the owners, said it was the only blind crayfish he had ever seen in the cave. They are abundant in the edges of quiet pools which make up the stream in the upper part of Cumberland Crystal Cave. I was informed by Mr. Clay Vest, the owner through whose courtesy my specimens were obtained, that the lower fork of the cave, referred to as "Pumpkin Center," was also inhabited by this crayfish. It is regrettable that a dam in the Cumberland River, now in the process of construction, will impound water over the cave entrance and make it inaccessible.

Differential Characters.—*O. pellucidus packardi* differs from *O. pellucidus pellucidus* by having a shorter acumen, smoother carapace, longer areola, more ovate antennal scale, and more strongly curved tips of the gonopod. *O. p. pellucidus* always has hooks on both the third and fourth walking legs but they are not always present on the fourth walking legs of *O. p. packardi.*

O. p. packardi differs from *O. pellucidus australis* (Rhoades) (1941) in having a much shorter areola and thicker, longer tips on the gonopods. Also *O. p. australis* has hooks only on the third walking legs.

Measurements of the type specimens are:—

	I	II	F
Total length	57.0 mm.	40.4 mm.	65.4 mm.
Length of carapace	25.8	23.0	30.2
Length of rostrum	5.2	5.2	7.7
Length of areola	11.2	9.4	12.5
Length of right cheliped	57.5	30.0	49.7
Length of right chela	24.5	13.5	23.5
Length of inner margin of palm	9.7	4.6	8.0
Length of movable finger	14.1	8.0	14.2
Length of abdomen	31.2	26.4	35.2
Width of carapace	11.4	9.3	12.9
Width of base of rostrum	3.6	3.1	4.2
Width of areola	2.2	1.9	3.4
Width of right chela	8.1	3.1	6.6
Width of 2nd abdominal segment	10.0	8.8	11.7

The type specimens have come from Cumberland Crystal Cave, at Alpine, Pulaski County, Kentucky. The allotypes, male, form II, and female, have been taken from collection U.S.N.M., No. 75821. The holotype, male,

form I, is U.S.N.M., No. 81310; the allotype, male, form II, is U.S.N.M., No. 81311; and the allotype, female, is U.S.N.M., No. 81312. Paratypes are deposited in the Museum of Comparative Zoology, the Museum of Zoology, University of Michigan, the collection of Horton H. Hobbs, Jr., University of Florida, and the collection of the writer.

I name this subspecies to honor Dr. Alphaeus Spring Packard, Jr., zoologist and naturalist, who made a great contribution to our knowledge of the North American cave fauna.

Orconectes kentuckiensis n. sp.

Kentucky Records:—OHIO RIVER SYSTEM—Tradewater River Drainage. Hazel Branch, 1 mi. s. of Sturgis, Union County. (3 m II; 1 f May 14, 1941). Tradewater River, 4 mi. s. of Sullivan, Crittenden County. (3 m II May 14, 1941). Piney Creek, 3 mi. w. of Shady Grove, Crittenden County. (3 m I; 1 m II; 7 f September 5, 1941). —TYPE LOCALITY.

Distribution and Ecology.—Orconectes kentuckiensis is a species apparently peculiar to the Tradewater drainage. The three localities are in the lower part of the drainage where there are heavy mud deposits. In the Tradewater River it was taken from under sticks where the mud was too soft and deep to wade. In Hazel Branch it was found in holes, apparently exposed tunnels of *Cambarus diogenes*, in hard clay which was covered in some parts with silt. At the type locality the specimens were taken from a mud and clay bottom under cover of brush and water willow (*Diantheris* sp.). *O. i. immunis* and *Palaeomonetes exilipes* were the associated decapods.

Description—Male, form I.—Rostrum long with straight, elevated, subparallel sides. Marginal spines prominent; acumen rather long with concave sides. Cervical groove somewhat sinuate and not markedly interrupted above well developed acute lateral spines. Areola usually as long, or slightly longer than one-third of the total length of the carapace (from 32.5 to 35.2 per cent) and from one-seventh to one-fifth as wide as long. Carapace usually cylindrical, but depressed in old individuals.

Antennal scale oblong with the margin gently receding from the strong apical to a nearly straight mesial margin. Free edges of the epistoma straight, not elevated, and ending in a blunt tooth. Chelipeds rather slender and chelae somewhat inflated. Fingers very long, not gaping, and slightly costate. Apposition edges not denticulate or only slightly so. Beard at the inner base of the immovable finger especially in young specimens. Inner margin of palm marked by seven to ten depressed tubercles and a secondary row of about the same number. Carpus with almost no furrow dorsally. One stout spine on the center of the inner face, a similar spine in the middle of the ventral anterior margin, and a smaller spine at the ventral articulation with the chela. Meros bispinose above anteriorly. Ventrally, the inner series of teeth is composed of six small spines and a large terminal one. The outer row is represented only by a large anterior terminal spine. Blunt recurved hooks on the third walking legs of the male, form I.

Gonopods reaching to the coxopodites of the second walking legs. Both tips recurved in the same direction and split for only a short distance at

the tip. The outer corneous tip is stout and blunt. The inner ramus is more strongly recurved and falls short of the outer. No shoulder present.

Male, form II.—Hooks on the third walking legs small and depressed. Gonopod with outer tip heavy and blunt and slightly recurved. Inner tip small, strongly recurved, and acute.

Female.—Annulus ventralis oval. Anterior margin depressed below the thoracic sterna. Behind this margin the surface of the annulus is depressed still further to form a wide fossa extending laterally to a small high area just inside each lateral extremity. The surface slopes up posteriorly to a general high area along the rim. Median furrow begins on the right as a wide sulcus about the end of a hook. It narrows and proceeds to the posterior rim in a sinuate line.

Measurements of the type specimens are:—

	I	II	F
Total Length	52.3 mm.	41.6 mm.	50.5 mm.
Length of carapace	25.4	20.5	23.8
Length of rostrum	7.8	6.7	6.8
Length of areola	8.4	6.4	7.9
Length of right cheliped	34.5	36.6	27.3
Length of right chela	17.6	13.2	12.7
Length of inner margin of palm	5.0	4.1	3.9
Length of movable finger	11.9	8.5	8.3
Length of abdomen	26.9	21.1	26.7
Width of carapace	12.4	9.4	12.0
Width of base of rostrum	3.6	2.7	3.4
Width of areola	1.2	1.0	1.7
Width of right chela	7.3	5.0	6.7
Width of 2nd abdominal segment	10.7	8.5	11.3

Type specimens have come from two localities. The holotype, male, form I, from Piney Creek, 3 mi. w. of Shady Grove, Crittenden County, Kentucky, is U.S.N.M., No. 81313; the allotype, male, form II, from the Tradewater River, 4 mi. s. of Sullivan, Crittenden County, Kentucky, is U.S.N.M., No. 81314; and the allotype, female, from Piney Creek, 3 mi. w. of Shady Grove, Crittenden County, Kentucky, is U.S.N.M., No. 81315. Paratypes are deposited in the Museum of Comparative Zoology and the collection of the writer.

Affinities.—*O. kentuckiensis* represents a more advanced stage in the series of the "Group rafinesquei." The tips are stouter and more differentiated and the annulus is more depressed as in *sloani* and other members of the "Group limosus." In this character it resembles closely *O. immunis immunis*. Furthermore, it is not difficult to see a possible affinity to the "Section of *C. virilis*" even in the gonopods of the male.

Orconectes propinquus jeffersoni n. ssp.

Kentucky Records: OHIO RIVER SYSTEM—Tributary to South Fork of Beargrass Creek, at Buchel, Jefferson County (to the Ohio). (3 m II; 6 f May 28, 1940). Tributary to Muddy Fork of Beargrass Creek, 2 mi. e. of Louisville corporation line, on USR-42, Jefferson County (to the Ohio). 1 m I; 2 f July 16, 1939) (4 m I; 5 m II; 15 f January 26, 1942).—TYPE LOCALITY.

Distribution and Ecology.—*O. propinquus jeffersoni* will probably be found distributed in the streams of Kentucky and Indiana and associated portions of the Ohio River in the area of the massive Niagara limestone. This is the ecological situation under which my specimens were taken. However, the influence of *O. sloani* and *O. indianensis* in southern Indiana may be keenly felt and, as a result, the species might be restricted to short tributaries of the river below the Falls of the Ohio.

Differential Characters.—*O. propinquus jeffersoni* differs from *O. propinquus* by having a much thicker gonopod with straight tips. The inner tips are more divergent than those of *O. p. propinquus* where the inner tips lie immediately ventral to the outer. The hands are slenderer and the annulus of the of the female is more prominently tuberculated.

It differs from *O. propinquus sanborni* (Faxon) (1884) in the presence of the median carina, more setiform and curved tips of the gonopods, and the more prominent tubercles of the annulus which is more deeply set in the sternum of the fifth segment.

Measurements of the type specimens are:—

	I	II	F
Total length	59.5 mm.	37.0 mm.	57.1 mm.
Length of carapace	28.2	17.3	27.4
Length of rostrum	7.5	4.5	7.3
Length of areola	9.8	5.6	9.3
Length of right cheliped	43.0	21.0	34.6
Length of right chela	24.3	9.7	16.9
Length of inner margin of palm	6.0	2.3	5.1
Length of movable finger	17.5	6.9	11.1
Length of abdomen	31.3	19.7	29.7
Width of carapace	14.8	8.7	13.7
Width of base of rostrum	3.8	2.5	3.7
Width of areola	1.7	1.3	2.2
Width of right chela	10.4	4.2	7.8
Width of 2nd abdominal segment	12.6	8.0	13.0

Type specimens have come from a Tributary to Muddy Fork of Beargrass Creek, 2 mi. e. of Louisville corporation line, on USR-42, Jefferson County, Kentucky. The holotype, male, form I, is U.S.N.M., No. 81316; the allotype, male, form II, is U.S.N.M., No. 81317; and the allotype, female, is U.S.N.M., No. 81318. Paratypes from the same locality are deposited in the Museum of Comparative Zoology, the Carnegie Museum, the Museum of Zoology, University of Michigan, and the collection of the writer.

ORCONECTES PROPINQUUS SANBORNI (Faxon) (1884)

Distribution and Ecology.—In Kentucky the species is found in the Ohio River* and Tygart Creek. It was the dominant crayfish everywhere in the Tygart but it was not encountered in the Little Sandy or the Big Sandy as

* The waters of the Ohio River to the low water mark on the north side is a part of Kentucky. This boundary was established during the original survey of the Northwest Territory.

inferred by Ortmann (1937:67). Since the major part of this drainage area lies in the *juvenilis* range it is to be expected that *juvenilis* would occur even in the lower reaches of the stream to the extent of dividing the *O. p. sanborni* range south of the Ohio.

O. p. sanborni is found in the Ohio River as far west as the mouth of the Little Miami. Thus, *O. p. sanborni* may be taken in the mouths of many small direct tributaries to the Ohio in Campbell, Pendleton, Bracken, and Mason counties.

Orconectes rusticus barrenensis n. ssp.

Kentucky Records:—OHIO RIVER SYSTEM—Green River Drainage. Barren River, at Beech Bend, 2 mi. n. of Bowling Green, Warren County. (4 m. I; 1 m II; 5 f January 27, 1942).—TYPE LOCALITY. "Barren River, Bowling Green, Warren County." (1 m II August 11, 1924, A. E. Ortmann, coll.). (Ortmann, 1931:77,79). Sulphur Creek, 1½ mi. e. of Hickory Flats, on the Simpson-Allen county line, Simpson County (to the Barren River). (2 m II; 2 f May 14, 1941). West Fork of Drake Creek, 1 mi. e. of Franklin County (to the Barren River). (2 m II; 6 f May 14, 1941). Peters Creek, at Pageville, Barren County (to the Barren River). (2 m II May 13, 1941). Beaver Dam Creek, 2 mi. e. of Bonayr, Barren County (to the Barren River). (5 m II; 1 f May 13, 1941). "Harrison Creek, 8 mi. s. of Glasgow, Barren County (to the Barren River)." (10 m II; 10 f Creaser & Decker) (M. M. Z.) Barren River, 2 mi. s. of Pageville, on the Barren-Allen county line, Allen County, (1 m I; 2 m II May 13, 1941). Green River, at Cave Island, Edmonson County. (3 m II; 6 f September 3, 1941).

Distribution and Ecology.—*O. rusticus barrenensis* is distributed through the Barren River and tributaries in Kentucky and probably Tennessee. It is found in the lower Green River in the vicinity of the Mammoth Cave. Streams flowing from the south into the Barren River, as Drakes Creek, seems to contain a transitional form but tributaries flowing in from the east and north have typical *barrenensis*. The species was taken mostly in fast water and its associate, *O. juvenilis*, was the usual pool species. In this respect it resembles *O. r. forceps*.

Differential Characters.—*O. rusticus barrenensis* differs from *O. rusticus rusticus* in having a well defined median carina and a much broader hand with more widely gaping fingers. It lacks the lateral spines on the carapace and the shoulder on the form I gonopod.

It is unlike *O. rusticus placidus* in having a shorter areola, more widely gaping fingers and the absence of inferior spines on the carpus.

It is also unlike *O. rusticus forceps* (Faxon) (1884) in that the fingers are not quite so widely gaping, the immovable finger is usually not defined from the palm by a constriction, and the rostrum is narrower and more deeply excavated.

O. r. barrenensis differs from *O. rusticus mirus* (Ortmann) (1931) by the much shorter and narrower areola and by the broad modified hand. The shoulder of the form I gonopod, which is present in *O. r. mirus*, is absent in *O. r. barrenensis*.

Measurements of the type specimens are:—

	I	II	F
Total length	30.5 mm.	49.4 mm.	36.6 mm.
Length of carapace	15.4	25.4	16.8
Length of rostrum	4.5	6.3	4.5
Length of areola	5.1	8.9	5.7
Length of left cheliped	22.6	42.8	22.6
Length of left chela	12.1	22.9	10.1
Length of inner margin of palm	4.2	7.3	3.2
Length of movable finger	8.3	16.2	6.9
Length of abdomen	15.1	24.0	19.8
Width of carapace	6.8	12.7	8.0
Width of base of rostrum	1.8	3.3	2.1
Width of areola	1.8	1.9	1.5
Width of left chela	5.7	10.5	4 6
Width of 2nd abdominal segment	6.2	10.0	7.8

The type specimens have come from two localities. The holotype, male, form I, from the Barren River, at Beech Bend, 2 mi. n. of Bowling Green, Warren County, Kentucky, is U.S.N.M., No. 81319; the allotype, male, form II, from Peters Creek, at Pageville, Barren County, Kentucky, is U.S.-N.M., No. 81320; and the allotype, female, from the Barren River, at Beech Bend, 2 mi. n. of Bowling Green, Warren County, Kentucky, is U.S.N.M., No. 81321. Paratypes from Beech Bend are deposited in the Carnegie Museum, the Museum of Comparative Zoology, the Museum of Zoology, University of Michigan, and the collection of the writer.

Variations.—The tributaries to the Barren River from the south contain a form which is an intergrade between *O. r. barrenensis* and *O. r. placidus*. The inferior spine of the carpus is represented by a nodule, the lateral spines of the carapace are minute, the hand is broadly oval, and the fingers are not so slender nor so widely gaping. The hand is a little more than twice as long as broad and the fingers are twice as long as the inner margin of the palm. The median carina is usually present but faint.

The specimens from the Green River do not have the fingers widely gaping and the immovable finger is defined by a slight constriction.

Further work should be done to ascertain the full distributional relationship of *O. r. barrenensis* with *O. r. placidus* and *O. r. forceps* especially in the Mussel Shoals area and the Great Allegheny Valley east of Walden Ridge.

ORCONECTES RUSTICUS PLACIDUS (Hagen) (1870)

Distribution and Ecology.—In Kentucky *O. r. placidus* is limited to the Cumberland River and tributaries. In the Little River and Red River the form is associated with other stream species and it does not reach the quantitative proportions it does in the Cumberland eastward where it is often dominant. In each locality the species was associated with limestone. As soon as the sandstones of eastern Kentucky appear in the stream bed the subspecies is reduced or terminated.

Taxonomic Remarks.—Typical *placidus* is found in the Nashville region and extends into southwestern Kentucky as a rather typical race.

In the upper Cumberland the subspecies is represented by a form with a broad heavy hand and shorter fingers. The spine on the middle of the ventral anterior margin of the carpus is quite strong in contrast to the almost obsolete spine of the western *placidus*. The median carina is mostly absent and the rostrum is broader as in typical *rusticus*. Specimens from Clinton and Wayne counties were marked in gay patterns of bright yellow, green, and red brown. The western *placidus* from Kentucky were marked in dull patterns of brown and black.

I do not choose to set aside a new subspecies because of the lack of material from the Cumberland in Tennessee where the status of the variety must ultimately be determined.

ORCONECTES RUSTICUS RUSTICUS (Girard) (1852)

Distribution and Ecology. — In Kentucky *O. r. rusticus* is distributed almost entirely on the exposed Ordovician, Silurian, and Devonian limestones of the Cincinnati Anticline. The westernmost record in Kentucky is from Fulton County in the Mississippi drainage. I possess specimens from Marshall County, in Clarks River drainage, which are close to the Green River form. In the Green River the species occurs above the mouth of the Rough River except in the Barren River where it is displaced by another subspecies. *O. r. rusticus* is the dominant species everywhere in the Salt River drainage and in Kentucky drainage below the mouth of the Red River. In the Licking the species occurs upstream as far as the Ordovician clays and limestones. I have a record from a tributary to the Ohio River in Mason County, however, I have been unable to collect the species in the river above U.S. Navigation Dam No. 36.

Taxonomic Remarks.—I unite under this species a group of drainage and local races all more or less distinguishable but commonly intergrading from one to the other. The typical *rusticus rusticus* is represented by those of northern Kentucky in the lower Kentucky and Licking rivers.

In the vicinity of Frankfort, in the Kentucky drainage, there is a local variety with a broader smaller chela which is mostly bearded. The lateral spines of the carapace are minute and the gonopod on the male, form I, is bent at the base of the rami which is characteristic of the Salt River *rusticus* also. The most striking superficial character is the golden yellow tips of the fingers which gently fade into the green of the hand without the usual darker band. Specimens from Flat Creek, Stony Creek, and Cold Spring Branch, Franklin County, belong to this variety.

The Salt River *rusticus* is most easily distinguished by the bent gonopods. The tip of the inner ramus is slightly incurved and very slender. The lateral spines of the carapace are rarely missing and the dark basal bands of the finger tips are always present.

From Otter Creek, Meade County, my specimens have very broad heavy hands and a trace of a median carina. The male, form I, from Doe Run, Meade County, has the outer tip noticeably recurved throughout its entire

length, the inner tip is compressed, and the shoulder is absent. My specimens from Brushy Fork, Hardin County, as well as the specimens from Elizabethtown, Hardin County, in the collections of the Museum of Zoology of the University of Michigan are similar to the Meade County material. These collections, differing widely in many respects, have a slightly longer and considerably wider areola.

The form from the Green River in the vicinity of the Mammoth Cave has a rather wide, short rostrum and the tubercles of the annulus are divergent so as to increase the apparent width between them. The hand is broad and rather short. *O. rusticus rusticus* was taken from the Green River in Ohio County with the annulus more open and the hand very slender.

West of the Cumberland and Tennessee in Clarks River drainage two specimens were taken which I have placed here. The rostrum, typical in outline, lacked the great excavation. The areola is within range of the length and width of the Green River form. The chelae are small, the fingers are short, and the whole cheliped seems primitive. A beard is present at the base of the immovable finger. The gonopods have the outer tip recurved and the inner tip ending bulbous and outcurved. It seems to be rare in the Jackson Purchase and after sufficient material is collected it may be deserving of a species status. Faxon's Moscow, Kentucky, record may also belong here.

One of Ortmann's criteria for a primitive species is the short wide areola. The *rusticus* of the western edge of the Cumberland Plateau possess the shortest and widest areola. From this region there is a slight tendency toward concentric variation (discussed under *C. b. bartoni*) in the direction of Cincinnati and vicinity. From this area in northern Kentucky up the Licking the areola becomes progressively shorter until collections from Fleming County measure exactly as the Green River specimens but the width is equal to those of the Boone and Kenton counties which are only one-half that of the *rusticus* of the western Cumberland Plateau. Proceeding up the Kentucky the areola becomes longer and slightly wider. In Franklin County specimens are occasionally encountered with an areola of more than 40.0 per cent.

ORCONECTES JUVENILIS (Hagen) (1870)

Distribution and Ecology.—The species is distributed over a wide area in southeastern and southern Kentucky. In the Green River it is associated with *O. r. rusticus* and *O. r. barrenensis*. In the east *rusticus* and *juvenilis* are seldom found associated except in the case of the *placidus-juvenilis* association in the Cumberland River. Roughly speaking, the species is distributed in the Barren and Green Rivers above their junction, in the Kentucky above the mouth of Dix River, in the Licking above Fleming County, and throughout the Little Sandy and Big Sandy. The species is common in the Upper Cumberland in southeastern Kentucky and might be taken in the Red or Little River in the southwest. Though there has been some question as to the crayfishes of the Salt River drainage I have been unable to find *juvenilis* in that area.

Taxonomic Remarks.—Orconectes juvenilis and its western form, *Orconectes putnami*, are here united under Hagen's species. Specimens from Grayson Springs are rather distinct from those of the Kentucky and Cumberland drainages but specimens from the headwaters of the Green River in Taylor, Adair, and Casey counties are all intergrades which can not be assigned definitely to one or the other.

There is a great variation in the width of the areola. Specimens from the headwaters of the Barren and Little Barren consistently run wider than those of any other region in the state. The areola becomes narrower northward, northeastward, and, to a degree, eastward. It is remarkable that the same amount of reduction in the width of the areola has been accomplished in the distance from Metcalfe County to Grayson County as from Metcalfe County to Greenup County. The cause of this is inferred in the previous statement. The Cumberland *juvenilis* has a wide areola, which is just a little narrower than the Green River form. The species apparently has developed a still narrower areola after passing into the Big Sandy from the Cumberland. Faxon's "*putnami*" records from southwestern West Virginia (1914:377) seem to further substantiate the theory that there may have been a divergence from a common type northward to produce the Grayson Springs *putnami* and eastward to produce the Barrenshe Creek *putnami*.

There are several local races which can be distinguished. In Estil, Powell, Lee, Clark, and Madison counties there is a form having a long rostrum with straight strongly converging sides and the surface is subplane. It is possible that M.C.Z., No. 3555 labelled "*Cambarus rusticus* var. ?" from Breathitt County belongs to this variety. The gonopods are not typical in many respects but the length is normal for *juvenilis*.

The Cumberland *juvenilis* is characterized by a long broad rostrum with straight parallel sides. The median carina is usually present in a well excavated surface. In these respects it resembles my topotypes of *putnami* from Grayson Springs except that the proportional width of the rostrum is much less. The Big Sandy and Little Sandy specimens show considerable similarity to the Cumberland.

The variety in the headwaters of the Green River, to which I have referred before, possess a very short but broad rostrum with the sides slightly concave to approach the *rusticus* character. The median carina is mostly absent. It bears little resemblance to the lower Green and the Barren River *juvenilis*. The same can be said of the relationship between this local form and the *juvenilis* eastward.

Orconectes bisectus n. sp.

Kentucky Records: OHIO RIVER SYSTEM—Brushy Fork, 1 mi. w. of Repton, Crittenden County (to Crooked Creek and the Ohio). (2 m II; 3 f May 14, 1941).—TYPE LOCALITY.

Distribution and Ecology.—Little can be said as to the distribution of the species but it will probably be found through the streams of the area around

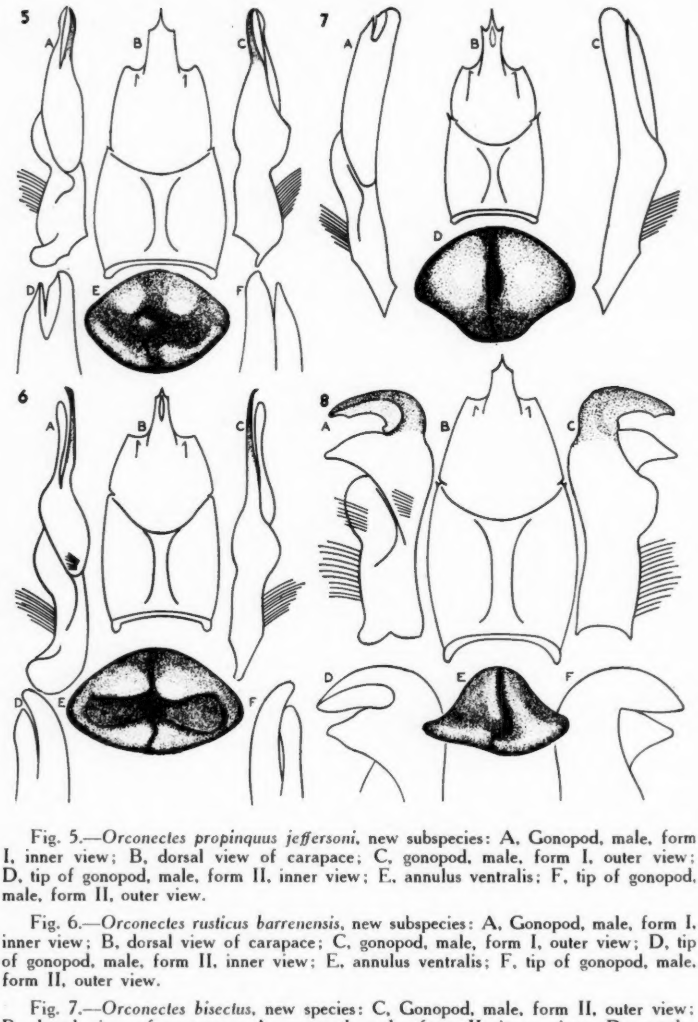


Fig. 5.—*Orconectes propinquus jeffersoni*, new subspecies: A, Gonopod, male, form I, inner view; B, dorsal view of carapace; C, gonopod, male, form I, outer view; D, tip of gonopod, male, form II, inner view; E, annulus ventralis; F, tip of gonopod, male, form II, outer view.

Fig. 6.—*Orconectes rusticus barrenensis*, new subspecies: A, Gonopod, male, form I, inner view; B, dorsal view of carapace; C, gonopod, male, form I, outer view; D, tip of gonopod, male, form II, inner view; E, annulus ventralis; F, tip of gonopod, male, form II, outer view.

Fig. 7.—*Orconectes bisectus*, new species: C, Gonopod, male, form II, outer view; B, dorsal view of carapace; A, gonopod, male, form II, inner view; D, annulus ventralis.

Fig. 8.—*Cambarus rusticiformis*, new species: A, Gonopod male, form I, inner view; B, dorsal view of carapace; C, gonopod, male, form I, outer view; D, tip of gonopod, male, form II, inner view; E, annulus ventralis; F, tip of gonopod, male, form II, outer view.

the mouths of the Cumberland and Tennessee rivers. It may also be found in the Tradewater River drainage but I am inclined to regard *O. kentuckiensis* as a competitive species. At the type locality the specimens were taken from a medium-sized stream with mud and rubble bottom and it was associated with *O. immunis immunis*.

Description—Male, form I.—Unknown.

Male, form II.—Rostrum of moderate length, wide and with converging, slightly concave margins. Surface moderately excavated with a very faint median carina. Marginal spines strong, acute, and divergent. Acumen long and slender. Cervical groove sinuate and interrupted over strong lateral spines. Branchiostegal spines acute. Areola of moderate length, varying from 32.2 to 34.4 per cent of the total length of the carapace, and moderately wide, from 12.4 to 16.6 per cent of its own length. Carapace subcylindrical and lightly granular.

Antennal scale ovate with a long apical spine. Epistoma rounded and obtuse at the tip. Chelipeds rather short and chelae rather long. Hand flattened, coarsely punctate, and strongly keeled externally. Inner margin bearing many small tubercules often of a spinous character. Fingers rather long, costate, setose, and slightly gaping. Carpus with a strong spine in the center of the mesial side and another mesial spine toward the anterior margin. There is a strong spine in the middle of the inferior face and another of similar size at the ventro-lateral articulation with the hand. The meros is acutely bispinose above anteriorly and the biserial row on the ventral side is represented by the two terminal spines and a few smaller spines all inclined considerably forward. Hooks on the third walking legs small and blunt.

Gonopods reaching to the coxopodites of the second walking legs. Tips straight or nearly so. Outer ramus thick with a blunt tip and slightly exceeding the inner slender outcurved tip. Rami united except at the tip.

Female.—Annulus ventralis with a high surface bisected longitudinally by a rather narrow fossa which widens posteriorly. The sinuate median furrow passes through the fossa.

Measurements of the type specimens are:—

	II	F
Total length	46.6 mm.	58.7 mm.
Length of carapace	22.8	29.0
Length of rostrum	6.0	8.5
Length of areola	7.5	9.8
Length of right cheliped	29.6	46.1
Length of right chela	14.5	19.7
Length of inner margin of palm	4.6	5.7
Length of movable finger	10.0	13.2
Length of abdomen	23.8	29.7
Width of carapace	10.5	13.6
Width of base of rostrum	3.4	4.0
Width of areola	1.2	1.2
Width of right chela	6.0	8.2
Width of 2nd abdominal segment	9.3	13.6

Type specimens have come from Brushy Fork, 1 mi. w. of Repton, Crittenden County, Kentucky. The holotype, male, form II, is U.S.N.M. No. 81322; the allotype female, is U.S.N.M., No. 81323. Paratypes are deposited in the Museum of Comparative Zoology and the collection of the writer.

Affinities.—In the absence of the male, form I, the systematic position is in some doubt. The tips of the gonopods are straight and united except for a short distance in the male, form II. It seems logically to go into Ortmann's "Section of *C. propinquus*." However, the annulus ventralis bears close resemblance to *O. creolanus* (Creaser) (1933). Since the species seems so distinct from the other known species I have included a description.*

ORCONECTES IMMUNIS IMMUNIS (Hagen) (1870)

Distribution and Ecology.—Orconectes immunis immunis is another addition to the Kentucky list. It is natural to expect the species in the sluggish, muddy, upland streams of western Kentucky. The crayfish is, for the most part, a stream form and the sloughs of the bayou counties did not yield *O. i. immunis*. This type of habitat is occupied largely by *Procambarus blandingi acutus*, but the same habitat occasionally yields *immunis* in the absence of *b. acutus* in the interior upland counties. In gravelly streams the species usually becomes a burrower in muddy banks as mentioned by Huntsman (1917: 131). The crayfish occupies the western coal field area and tributaries to the Mississippi in the Jackson Purchase. The short rapid streams flowing into the Cumberland and Tennessee do not provide suitable habitat. In the Clarks River drainage *Procambarus blandingi acutus* and *Cambarus diogenes* are abundant and *immunis* seems to be a minor species. The sandy and muddy streams of the bayou counties do not yield the quantitative population of *immunis* as found eastward.

Taxonomic Remarks.—I have not been able to separate the *immunis immunis* from *immunis spinirostris* in western Kentucky. The spines of the rostrum are a juvenile character as Ortmann has stated (1931:93-94). Faxon's character of the shorter areola is not outstanding but blends into the measurements of *immunis immunis*. In strict adherence to Faxon's character, specimens are removed from collections without regard to locality or other morphological characters so that, as Creaser has stated (1933:14), western Kentucky and Tennessee appear to be a region of intergrades. Though some specimens have a heavier and more bearded claw, a higher, shorter posterior section of the carapace, or small spines on the rostrum the great inconsistency among these characters has led me to place my specimens in *O. immunis immunis*.

The areola of my specimens vary from 31.5 to 35.3 per cent of the total length of the carapace. Specimens of a collection run remarkably constant in this measurement but wide variation often occurs between collections of only a few miles apart.

* This species was discovered late in the preparation of this paper and the possibility of a return to Crittenden County for additional material was dismissed because of the present national emergency.

Marginal spines of the rostrum are mostly present in juveniles and usually absent in adults. In the Green River, adults often bear marginal spines. Strangely, individuals of this race have the longest and shortest areolae I have measured for the species in western Kentucky. The length varies from 31.5 to 35.0 per cent.

In the area between the mouths of the Tradewater and the Green rivers specimens were often encountered with a very robust posterior section of the carapace and the hand was usually heavier. However, the areola was not necessarily shorter. These were associated and often intergraded with the normal form.

ORCONECTES COMPRESSUS (Faxon) (1884)

Distribution and Ecology.—Orconectes compressus, a new species to the Kentucky list, has been reported from the type locality in Alabama (Faxon 1884:128) and Mississippi (Goodnight 1940:222-223). It is a common species of the lower Tennessee and tributaries.

In Kentucky one record was obtained from Little River, a tributary to the Cumberland. The species should be present in the tributaries of the Red River flowing south from Christian, Todd, and Logan counties. These two streams flow from the cavernous uplands and are mostly spring-fed. The extension of the species northward along the Cumberland is retarded by a radical change in ecology as indicated by the presence of *O. b. acutus* and others.

The species has crossed the drainage divide between the Cumberland and Barren rivers. The species is common to abundant throughout the Barren River drainage.

O. compressus is easily mistaken for the immatures of associated species in seined collections and their color blends so perfectly with the gravelly stream beds that they are difficult to detect for hand collecting. These characters combined with their habit of remaining motionless on the bottom when disturbed may account to some extent for the obscurity of the species.

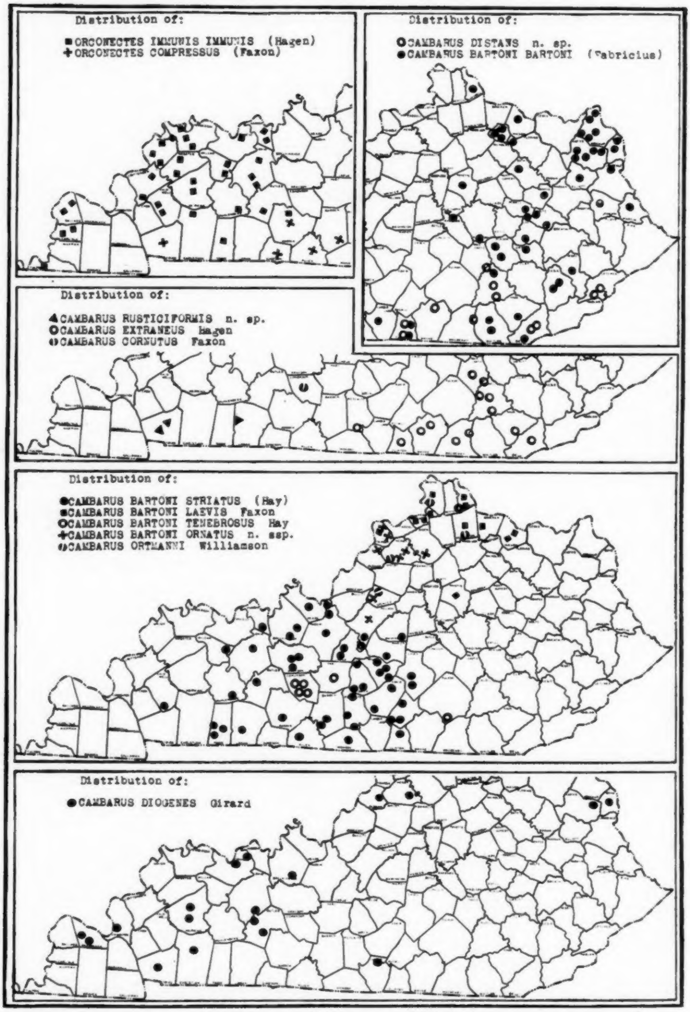
Taxonomic Remarks.—My Kentucky specimens differ only slightly from the collections taken in Lauderdale County, Alabama. There is a tendency toward stronger spines and the rostrum is slightly broader near the tip. The fingers are usually, though not always, a little longer.

Cambarus rusticiformis n. sp.

Kentucky Records:—OHIO RIVER SYSTEM—Cumberland River Drainage. Mud Fork, 3 mi. n. of Cadiz, Trigg County (to Little River). 1 m II; 3 f (immature) May 15, 1941). Little River, 1/2 mi. w. of Cadiz, Trigg County. (1 m I; 2 f May 15, 1941). —TYPE LOCALITY. Whippoorwill Creek, 3 mi. s. of Gordonsville, Logan County (to the Red River). (1 m II May 15, 1941).

Distribution and Ecology.—Cambarus rusticiformis is known only from the cool streams of the lower Cumberland drainage. The distribution probably extends southward and eastward into the Nashville region. It inhabits the fast water of medium and large streams and lives under rubble. In both localities

in Trigg County my specimens were taken from fast, cold, stony riffles. Its associates were *O. compressus* and various species of darters and sculpins. At the Logan County locality it was taken in company with *O. r. placidus*, *C. b. striatus*, and darters on a solid rock and rubble riffle.



Description—Male, form I.—Rostrum of moderate length, well excavated, and usually rather narrow. Margins decidedly concave around the eyes and ending anteriorly in upright corneous tips but sometimes flattened nodules. Acumen short and broadly triangular. Sub-orbital angle nearly absent. Cervical groove deep, sinuate and not interrupted on the sides above acute lateral spines. Branchiostegal spine minute. Areola long and moderately wide. Length varying from 37.8 to 39.9 per cent of the total length of the carapace. Its width is from one-sixth to one-fourth of its own length but usually wider than one-fifth. Carapace depressed making the transverse outline subquadrangular. Smooth above and thickly granulose on the sides.

Flagella normal. Antennal scale broad with the inner margin uniformly rounded except where it becomes straight a short distance behind the long, stout, acute apical spine. Epistoma oval in outline with a stout terminal tooth. Chelipeds and chelae rather large. Hands inflated and covered above and below with coarse punctations. Inner margin serrate and bearing seven to ten depressed tubercles. Fingers costate, cylindrical, and often gaping slightly. Apposition edges of both fingers denticulate from base to tip. A conspicuous denticle about midway on each finger. Carpus with a stout spine on the center of the inner face and a smaller one on the inferior surface in the middle of the anterior margin. Spines of the dorsal anterior region of the meros variable but always one spine with either a tubercle of a second spine. Ventrally, inner series of biserial row of spines present with a well developed anterior one. Outer series represented by a stout terminal spine and a smaller one following. Hooks of third walking legs large and plate-like. Hooks of the fourth walking legs wanting.

Gonopods with tips recurved. Tip of outer ramus rather slender and corneous. Tip of inner ramus bulbous toward the base and terminating acutely.

Male, form II.—Hooks of third walking legs reduced. Tip of outer ramus heavier and fleshy. Tip of inner ramus triangular in outline from lateral aspect and not so acute.

Female.—Annulus ventralis elliptical. Anterior wall not defined and posterior wall high. Prominent ridges along each side of the straight anterior course of the median furrow. A little behind the center the furrow curved to form a heavy hook to the right.

Measurements of the type specimens are:—

	I	II	F
Total length	61.5 mm.	61.8 mm.	57.4 mm.
Length of carapace	31.5	30.8	28.8
Length of rostrum	5.6	5.9	6.6
Length of areola	12.6	12.2	11.1
Length of right cheliped	47.8	43.6	43.6
Length of right chela	26.7	22.6	21.7
Length of inner margin of palm	10.5	6.7	8.9
Length of movable finger	15.3	13.8	12.5
Length of abdomen	30.0	31.8	28.6
Width of carapace	17.0	17.3	16.0
Width of base of rostrum	4.5	4.5	4.0
Width of areola	2.4	2.2	2.1
Width of right chela	12.7	9.8	10.6
Width of 2nd abdominal segment	14.7	14.9	14.3

The type specimens have come from two localities. The holotype, male, form I, from Little River, ½ mi. w. of Cadiz, Trigg County, Kentucky, is U.S.N.M., No. 81324; the allotype, male, form II, from Mud Fork, 3 mi. w. of Cadiz, Trigg County, Kentucky, is U.S.N.M., No. 81325; and the allotype, female, from Little River, ½ mi. w. of Cadiz, Trigg County, Kentucky, is U.S.N.M., No. 81326. Paratypes from Little River and Whippoorwill Creek are deposited in the Museum of Comparative Zoology and the collection of the writer.

Affinities.—The species is closely related to *Cambarus cornutus* but it is distinguishable from it by the shorter and normal flagella of the antennae and the rounded margin of the antennal scale. It differs from *Cambarus girardianus* by having a shorter acumen, sub-orbital angle wanting, a narrower areola, shorter antennae, and the absence of the beard at the base of the immovable finger. Since the rostrum closely approaches the shape of *Orconectes rusticus* the name, *rusticiformis,* seems applicable.

CAMBARUS CORNUTUS Faxon (1884)

Distribution and Ecology.—This unusual species is known by a single specimen from the type locality. Additional material has been sought by collectors of crustacea without success. *Cambarus rusticiformis,* a close relative of *C. cornutus,* occurring in the Red and Little rivers is always associated with riffles and limestone or rubble. This Green River *Cambarus* may have similar ecological requirements.

CAMBARUS EXTRANEUS Hagen (1870)

Distribution and Ecology.—The general distribution of *Cambarus extraneus* includes the middle Tennessee valley east of Walden Ridge and west of the Smokies and the Blue Ridge. After Williamson's collection at Livingston the known range was extended northward considerably.

It seems that this species has passed into the Upper Cumberland from the Tennessee by way of South Fork. Quantitatively, the species reaches its climax in the Laurel and Rockcastle rivers as far as the Cumberland drainage of Kentucky is concerned. It can be collected not only in the large streams but also in small rubble streams where it is associated with *Cambarus bartoni.* A female bearing "eyed" eggs was collected in Traces Branch, Laurel County, on August 15, 1939.

Taxonomic Remarks.—Ortmann discussed the *extraneus* complexity of the Cumberland Mountains (1931:102). There is almost no variation from the characters described by Ortmann for the upper Cumberland race. There is an occasional specimen without lateral spines on the carapace and the specimen from Beaver Creek has but a single row of tubercles on the inner margin of the palm.

Cambarus distans n. sp.

Kentucky Records:—OHIO RIVER SYSTEM—Cumberland River Drainage. "Stream, 3 mi. s. of Albany, Clinton County (to Wolf River)." (1 m II; 1 f July 28, 1931, Creaser & Delavan, coll.) (M. M. Z.). Gross Creek, 8 mi. s. of Albany, Clinton

County. (4 f May 29, 1941). "Meadow Creek, 1/2 mi. e. of Mill Springs, Wayne County." (1 m I; 6 m II; 2 f July 29, 1931, E. P. Creaser, coll.). (M. M. Z.). "Small streams tributary to Rockcastle River, Livingston, Rockcastle County." (3 m II; 1 f June 21, 1904, E. B. Williamson, coll.). (Ortmann, in Williamson, 1905:310). Traces Branch, 2 mi. s. of London, Laurel County (to Laurel River). (1 f August 15, 1939). Cumberland River and a small tributary, just above Cumberland Falls, McCreary County. (2 m I; 2 m II; 4 f October 8, 1941). (3 m I; 4 m II; 3 f October 20, 1935, C. L. & L. C. Hubbs, coll.). (M. M. Z.) "Stinking Creek, near mouth in Cumberland River, Knox County." (2 m I; 2 m II; 2 f October 19, 1935, C. L. & L. C. Hubbs, coll.). (M. M. Z.). Cumberland River, 1 mi. s. of Pineville, Knox County. (2 f August 15, 1939). (1 m II October 20, 1935, C. L. & L. C. Hubbs, coll.). "Cumberland River, Orby, Bell County." (2 m I; 3 f September 10, 1913, A. E. Ortmann, coll.). (Ortmann, 1931:132). Poor Fork, 1 mi. e. of Harlan-Letcher county line, Letcher County. (1 m II; 1 f October 8, 1941). Poor Fork, 1 mi. w. of Partridge, Letcher County. (1 m I; 2 f October 8, 1941).

Distrbution and Ecology.—*Cambarus distans*, listed by Ortmann as No. 2 of his "regionally restricted" forms of *C. bartoni*, is distributed through the upper Cumberland drainage and South Fork (See Ortmann 1931:136). Specimens are frequently found in the North Fork and the Middle Fork of the Kentucky with a longer, narrower, more converging rostrum and with a wide areola. The gonopod and hand are typically *bartoni*.

In Kentucky *C. distans* is distributed generally in the Cumberland and Ortmann, in Williamson reported this form from the Rockcastle River drainage. I have taken a fairly typical collection of the species in Clinton County and the Museum of Zoology, University of Michigan, has a collection from the Wolf River drainage. These indicate that Faxon's Albany record may

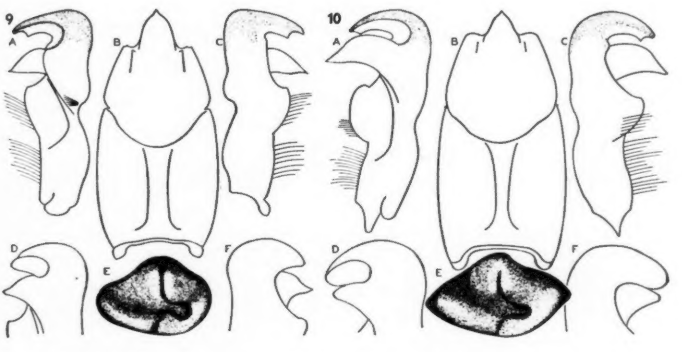


Fig. 9.—*Cambarus distans*, new species: A, Gonopod, male, form I, inner view; B, dorsal view of carapace; C, gonopod, male, form I, outer view; D, tip of gonopod, male, form II, inner view; E, annulus ventralis; F, tip of gonopod, male, form II, outer view.

Fig. 10.—*Cambarus bartoni ornatus*, new subspecies: A, Gonopod, male, form I, inner view; B, dorsal view of carapace; C, gonopod, male, form I, outer view; D, tip of gonopod, male, form II, inner view; E, annulus ventralis; F, tip of gonopod, male, form II, outer view.

belong here (1898:649). At the type locality the specimens were taken from the river as well as a small tributary.

Description—Male, form I.—Rostrum of moderate length and subplane with sides converging strongly and gently contracting into an acumen of moderate length. Sub-orbital angle spinose. Cervical groove sinuate and interrupted on the sides near small tubercles. Branchiostegal spines minute. Areola of moderate length varying from 35.4 to 39.8 per cent of the total length of the carapace and its width is from one-fifth to one-fourth of its own length. The carapace is somewhat depressed and the sides are granulose, reaching tubercular proportions in the hepatic region.

Antennal scale broadly obovate or spatulate with a stout apical spine. Epistoma rounded on the free edges. Chelae rather long and stout. Fingers strongly costate and a little more than twice as long as the inner margin of the palm. Apposition edges of the fingers marked by three or four denticles at the base of each finger. The setae along the edges are modified to form small close fitting vertical plates for the remainder of the distance. The fingers are somewhat gaping in older specimens. External border of the immovable finger keeled and the hand slightly inflated. Inner margin of the palm marked by six to nine prominent tubercles of almost spinous proportions. This row often extends onto the posterior margin of the hand for a short distance. The second row is always present but the tubercles may not be conspicuous. Carpus rather long and deeply furrowed dorsally. Inner face bearing one long, recurved, acute spine centrally and a prominent sub-basal tubercle. The inferior face is marked by a large spine in the center, a smaller tubercle in the middle of the anterior margin, and one or two tubercles between these and the median central spine. The meros is marked dorsally by two tubercles on the anterior end and the spines of the inferior biserial row are stout. The inner row, exceeding in number, has a strong terminal spine and the outer row is short with a moderate terminal spine. The outer spine of the anterior margin is represented by a prominent blunt lobe. Hooks of the third walking legs prominent and straight and hooks wanting on the fourth.

Gonopods recurved as in *C. bartoni*. Tips widely separated with inner fleshy tip appearing halfway between the ventral shoulder and the corneous hook. The fleshy tip is bulbous and acute and is made more strongly recurved by its own asymmetry.

Male, form II.—Hooks of the fourth walking legs reduced to erect tubercles. Gonopods with outer tip stouter and the inner tip acute and symmetrical but still appearing halfway between the ventral shoulder and the tip of the outer ramus.

Female.—Annulus ventralis nearly circular in outline. Anterior wall not elevated and only slightly raised in two ridges which follow the anterior straight course of the median furrow. A long, thick, blunt lobe extends into and almost under the high area in the posterior left section. The furrow returns to or beyond the median line and proceeds to the posterior border. The species exhibits a reversal of this pattern.

Measurements of the type specimens are:—

	I	II	F
Total length	73.7 mm.	54.2 mm.	71.6 mm.
Length of carapace	38.7	26.3	35.2
Length of rostrum	7.2	5.3	6.0
Length of areola	15.5	9.6	13.8
Length of right cheliped	55.6	34.7	49.5
Length of right chela	27.6	15.8	25.3
Length of inner margin of palm	8.5	5.1	8.4
Length of movable finger	18.4	10.1	15.8
Length of abdomen	35.0	27.9	36.4
Width of carapace	20.6	13.7	18.0
Width of base of rostrum	5.9	2.9	5.3
Width of areola	3.5	2.4	3.3
Width of right chela	12.7	8.5	12.2
Width of 2nd abdominal segment	16.6	12.0	16.6

Type specimens have come from the Cumberland River and a small tributary, just above Cumberland Falls, McCreary County, Kentucky. The holotype, male, form I, is U.S.N.M., No. 81327; the allotype, male, form II, is U.S.N.M., No. 81328; and the allotype, female, is U.S.N.M., No. 81329. Paratypes from the same locality are in the Carnegie Museum, the Museum of Zoology, University of Michigan, and the collection of the writer.

Affinities.—The species is closely related to the *bartoni* of the upper Tennessee drainage in Virginia. The streams of the high Cumberland Mountains of eastern Kentucky, southwestern West Virginia, and along the northwestern border of Virginia interlock so that the crayfishes have had an opportunity to cross the drainage divides. Differentiation has progressed to a greater extent in the Cumberland than the Kentucky or the Big Sandy as will be seen in the discussion of *C. b. bartoni*. Toward the western part of the range, as shown by my collections, there is a tendency away from typical *diistans* toward other species, yet undescribed, from the Cumberland drainage in Tennessee.

CAMBARUS BARTONI BARTONI (Fabricius) (1798)

Distribution and Ecology.—*Cambarus bartoni bartoni* is widely distributed over eastern United States. It is a species of small spring fed streams and the springs at their sources. In medium and large streams the species is occasionally encountered in the riffles. It is likely that these specimens represent a faunal loss of smaller tributaries of very steep gradient. Over the extensive range many local forms have arisen. In Kentucky several minor races are apparent in the various drainage areas.

C. b. bartoni is distributed over the eastern half of Kentucky from Covington south to Lexington and down the Green and Cumberland drainage divide to the Tennessee line. It is superseded in many places in this area by related species and subspecies.

In the medium and large streams of northeastern Kentucky there is an unusual form living naturally in riffles. It differs from the small stream *bartoni* of the area and, therefore, does not seem to be accidental specimens from upstream.

Taxonomic Remarks.—By these remarks several local varieties are distinguished. In the Rockcastle River drainage there is a form of *bartoni* possessing a longer narrower areola. It is from 37.0 to 40.5 per cent of the total length of the carapace (See Ortmann 1931:136). This proportion is found also in the specimen from Norris Branch, Cumberland County. The *bartoni bartoni* typical of the Cumberland drainage elsewhere has a slightly shorter and wider areola.

The *bartoni bartoni* of the Big Sandy and the upper Kentucky are closely related to the Cumberland *bartoni* as far as the measurements of the areola are concerned, however, the rostrum shows little relationship. It must be borne in mind that the areola becomes longer and narrower as the distance is increased from the Great Smoky Mountain area. The concentric quality of the isometric lines is modified by the streams flowing from that region. In collections taken from most counties from the southern Appalachians to northwestern Ohio the length of the areola increases more or less uniformly from 30.0 and 32.0 per cent to 40.0 and 42.0 per cent. There is not such a remarkable gradient in the variation of the width though it is very evident. Thus, *C. b. bartoni* of the Licking, Kentucky, and Cumberland are subject to this variation.

The *C. bartoni* of the Big Sandy, Little Sandy, and Tygart Creek differ considerably from those of the approximate streams to the west. The typical Sandy River form has a slightly shorter areola as found in the Cumberland drainage. Furthermore, the areola is very wide as in the western Virginia *bartoni* which are suggestive of the *montanus* group. It must be remembered that *C. montanus montanus* has been reported from the headwaters of the Big Sandy in West Virginia and it is reasonable to expect approaching forms, if not the true *montanus*, lower in the drainage. The actual status of this wide areoled form depends upon its distribution and connections in western and southwestern West Virginia. Ecologically, it resembles the *montanus* group since it inhabits riffles of medium and large streams.

There are several specimens from northeastern Kentucky, especially in the Tygart Creek drainage, having a rather narrow areola. In this respect they approach *C. b. laevis* but the areola is not as narrow or as long as the fairly typical *laevis* from northern Kentucky. Also, the antennal scale is broadly obovate and not small and oblong as in *laevis*. Specimens from the lower Licking and the Ohio valley in Mason, Robertson, and Fleming counties show trends toward *laevis*. The rostrum is contracted gently into a longer acumen and the areola is longer and narrower. They approach the *laevis* even more than those mentioned from the Tygart Creek watershed.

I have three specimens of *bartoni* which have very long rostra with the sides strongly converging and without a definite acumen. The significance of this peculiarity is doubtful for the normal form was taken at the same time. There seems to be no other morphological difference. A specimen from Laurel Fork, Leslie County, has, in addition to the long rostrum, lateral spines on the carapace and a double row of tubercles on the inner margin of the palm.

Several collections from the Red River are rather constant in the shape of the rostrum. It is a little shorter and gently contracted into a long acumen. A specimen from Brier Creek, Whitley County, has a broad low median carina and two additional spines on the mesial side of the carpus. A collection from Gross Creek, Clinton County, contained a specimen resembling *C. b. cavatus,* listed here as *C. b. bartoni, C. distans,* and *C. b. striatus,* in addition to fairly typical *C. b. bartoni.* This is the greatest variation within a collection of *bartoni* I have found in Kentucky.

CAMBARUS BARTONI STRIATUS (Hay) (1902)

Distribution and Ecology.—In Kentucky, where it has not definitely been known previously, *Cambarus bartoni striatus* is represented by several local varieties and races which intergrade into each other to a greater or lesser degree. I have not seen my way clear to create new subspecies and, furthermore, I have followed Ortmann in uniting *Cambarus graysoni* with *C. b. striatus* for reasons which will be discussed presently.

Small streams of the Cumberland, Green and Salt river drainages in Kentucky are inhabited by the subspecies. It is represented by an atypical form in the headwaters of the Barren River and here the species is found in small burrows under stones in the riffles of medium-sized streams. In the lower Green River drainage there is a form close to *C. diogenes* which occupies short vertical burrows in the bank near the water's edge.

Taxonomic Remarks.—The specimens best representing the species in the state are from the Red River tributaries in Todd and Logan counties. They can be immediately distinguished from those of the Green and Salt rivers by the presence of lateral spines of the carapace and the longer and narrower rostrum with a rather long acumen. The specimens from Lost River in the Barren drainage also possess lateral spines and are close to the Cumberland *striatus* with respect to granulation and armature of the cheliped.

The typical Barren River *striatus* has a long, broad, excavated rostrum with the sides nearly parallel and contracting into a short acumen. The lateral spines of the carapace are typically absent. The form recalls characters of the Cumberland *C. b. bartoni* from the east and southeast. The areola is slightly shorter and narrower than the Red River *striatus.* The specimens taken in this drainage were mostly very dark green and could be distinguished superficially on that basis.

North of this area in the headwaters of the Green River the form of *striatus* has a short, slightly excavated rostrum with the sides converging in straight lines and then contracting more strongly into a longer acumen. The areola is shorter, as in *C. b. bartoni,* and narrower than either the Red River or Barren River *striatus.* In some specimens from the Little Barren River the areola was exceptionally long.

In the Salt River watershed and the valley of the Ohio the species is represented by a race with a longer, slightly broader areola and with smoother

chelae and carapace. However, in Dripping Springs Cave and the issuing stream, Tioga Creek, Hardin County, specimens were taken which had more prominent tubercles on the inner margin of the palm than the Cumberland form. The rostrum of these specimens resembled the Barren River *striatus*. The variation of the subspecies along its northern limit is exceedingly great, both locally and individually.

In regard to *Cambarus graysoni*, synonymous with *C. b. striatus*, it seems to be one of the local variations existing north of the Green River. The rostrum resembles the Green River headwater form but is a little shorter and less converging. It occasionally approaches the Barren River *striatus* in this regard. The areola according to Faxon (1914:393-394), is 38.9 per cent, which is somewhat longer than the *striatus* of the headwaters. Also, the areola is slightly wider in the Bear Creek form. Specimens from Cedar Lick, Grayson County, were identical and the collection from Jewells Creek, Breckenridge County, was very close to this form. "*Cambarus graysoni*" is, then, a local variety equivalent to the others listed here.

A collection from Doe Run, Meade County, resembles the Red River *stiratus* by having acute lateral spines on the carapace. It, likewise, has a rather long rostrum but with the sides suddenly contracted into an acumen of moderate length.

I possess four collections of mostly small individuals of a variety from the lower Green River drainage which is probably a distinct species. The adults at hand show a great affinity to the *diogenes* section. It is close to *ortmanni* in measurements of the carapace. The gastric region is high and the rostrum is decurved. In outline the rostrum is rather broad and elongated with the sides gently converging for most of their length. The acumen is not defined The annulus is nearly circular, a characteristic associated with the *diogenes* section. The hand is very similar to *striatus* with two rows of prominent tubercles on the inner margin of the palm. The areola is identical with *striatus* in length but the width is slightly narrower. I do not describe this form because of the lack of mature specimens.

Ortmann separated *striatus* and *laevis* on the basis of the granulation on the sides of the carapace and the distinctness of the tubercles on the inner margin of the palm. These characters are sufficient to distinguish the Cumberland specimens from the Wabash material but the specimens from the Cumberland Plateau between the Green River and the Ohio can not be separated on this basis. A specimen from Sinking Creek, Breckenridge County, has a strong row of tubercles on the inner margin but the granules of the carapace are minute. Furthermore, specimens considered as otherwise good *laevis* from northern Kentucky will have the inner margin occupied by three or four very large tubercles. Two rows of tubercles on the hand are rather typical of the *striatus* throughout its range in western Kentucky. The areola of *striatus* is usually wider than *laevis*, except in the headwaters of the Green River and Barren River, where the species can be separated by the shorter, broader rostrum with a short acumen. The rostrum of *striatus*, except the Cumberland

form, does not contract gently into a long acumen. The carapace is usually granulose but the size of the tubercles on the inner margin of the hand is not a good character for distinguishing *C. b. striatus* and *C. b. laevis* in Kentucky.

CAMBARUS BARTONI LAEVIS Faxon (1914)

Distribution and Ecology.—Shull (1909:301) records *Cambarus bartoni* from Fayette County "having a narrower areola, less spiny carpus, and a shorter but broader rostrum than the eastern form." Ortmann states that they agree with Mitchell County, Indiana, specimens. This is somewhat south of the range indicated by my collections but it is quite likely that the streams of the blue grass upland would furnish suitable ecology. The easternmost record in Kentucky is from Mason County. Throughout its range in the east and southeast it is associated with other forms of *bartoni.* It was taken from small rocky streams and seldom occurred in cold spring-fed runs.

Taxonomic Remarks.—The species can be distinguished from *striatus* to the southwest by the longer rostrum and longer acumen. The antennal scale is smaller and narrower and the inner fleshy tip of the gonopod in the male, form I, is asymmetrical as in *ortmanni.*

Specimens from the tributaries to the Ohio below the mouth of the Kentucky are intergrades between this species and *striatus.* They are very smooth, the rostrum is rather short and broader near the tip, and the tubercles on the inner margin of the hand are depressed.

In caves and associated waters of Carter County specimens were often found with narrow areolae though not so narrow as the Licking specimens. The rostrum is short as well as the acumen and the antennal scale is not reduced. Near Falmouth some individuals have stronger tubercles on the inner margin and the areola is wider as in *striatus.* Indiana and Ohio specimens usually have two rows of tubercles on the hand. In the Kentucky specimens one row is typical but two rows are occasionally found. In Gallatin County one collection had the subquadrangular robust carapace of *ortmanni.*

CAMBARUS BARTONI TENEBROSUS Hay (1902)

Distribution and Ecology.—*Cambarus bartoni tenebrosus* is known chiefly from the cold rocky streams of the caverns of the Mammoth Cave region. It can be taken occasionally in surface streams which connect with the underground drainage. The species was not found associated with *C. b. striatus,* the prevailing surface *bartoni* of the area.

In Cumberland Crystal Cave, Pulaski County, several specimens were taken which closely resemble the *tenebrosus* of the Mammoth Cave. They are grouped here with the cave subspecies from Edmonson County though they may have had a different origin.

Taxonomic Remarks.—It is unusual that Faxon did not elaborate upon *C. b. tenebrosus* in his, "Notes on the Crayfishes. . . ." (1914). He refers to

it under *C. b. laevis* (p. 392) and in his list of described species (p. 424) but does not deal with it as the other species received at the United States National Museum "since my last paper on these animals" (1898).

This subspecies is not well understood in its relation to the surface *bartoni* of the cave area. Hay described (1902:232-245) and compared it with *C. b. bartoni* from the vicinity of Philadelphia. As a result he concluded that his species differed in having a more converging rostrum, lateral spines on the carapace, a longer areola, a cylindrical carapace, long and slender antennae, reduced eyes, and the spines in general more developed. Had he compared the cave specimens with *C. b. striatus,* the normal surface *bartoni* of the county, he could have said no more than: Lateral spines of the carapace present, antennae longer and slenderer, eyes reduced, and spines in general more developed. It is apparent that these characters are commonly found in most cave crayfishes and represent an adaptation for cave life. However, the modification has not been so great as to make the species unable to survive in surface streams. I have collected specimens from a small tributary to the Green River, Edmonson County, which are identical with the specimens from the Mammoth Cave. I will discuss under *C. b. ornatus* the part that this partial transformation may have had in developing a surface species from the cavernous lands to the north.

From Cumberland Crystal Cave, Pulaski County, I have a set of specimens which closely approximate the *C. b. tenebrosus* from the Mammoth Cave. The degree of similarity is surprising considering the different drainage and distance between the two localities. Furthermore, the Pulaski County form seems to have arisen from *C. b. bartoni* and not *C. b. striatus* as *tenebrosus* has done westward. The areola is slightly shorter and wider than the Mammoth Cave specimens but the ratios are very near those of the Rockcastle River *bartoni bartoni.* The rostrum of the Cumberland *tenebrosus* is less converging, the margins contract rather sharply into an acumen of moderate length, and the surface is more deeply excavated. The lateral spines of the carapace as well as the armature in general is a little stronger and more acute. Thus, we may find similar cave species being produced under similar conditions, or a case of parallelism. Hay's description is general enough to include this form easily by the lateral spines on the carapace, the long areola, long antennae, and reduced eyes. In the Mammoth Cave *tenebrosus* the areola is from 38.5 to 40.0 per cent of the total length of the carapace and its width is from 10.0 to 17.0 per cent of its own length. In the Cumberland Crystal Cave *tenebrosus* the areola is from 35.4 to 40.5, mostly 37.0 to 39.0 per cent, and its width is from 16.8 to 19.2 per cent. It may be possible after an examination of the male, form I, to separate this record from *C. b. tenebrosus.*

Cambarus bartoni ornatus n. ssp.

Kentucky Records:—OHIO RIVER SYSTEM—Salt River Drainage. Spring, "My Old Kentucky Home," Bardstown, Nelson County (to Rolling Fork). (1 f May 28, 1940). Small run, 5 mi. s. of Mt. Washington, Spencer County. (1 m I; 1 m II May 28, 1940). Organ Creek, 1½ mi. w. of Sligo, Oldham County (to the Ohio), (1 m II March 23, 1939). Barebone Creek, sw. of Bedford, Trimble County (to the Ohio).

(1 m II; 1 f March 23, 1939). Little Kentucky River Drainage. Ellis Branch, 4 mi. sw. of Carrollton, Carroll County. (1 m I; 2 m II; 2 f March 23, 1939).—TYPE LOCALITY. Hardy Creek, 3 mi. e. of Bedford, Trimble County. (1 m II March 23, 1939). Kentucky River Drainage. Head of Drennon Creek, 3 mi. w. of North Pleasureville, Henry County. (1 m II March 23, 1939). Five Mile Creek, 3 mi. nw. of Bethlehem, Henry County. (1 f March 23, 1939). Tributary to Severn Creek, 3 mi. n. of Monterey, Owen County. (1 m II; 2 f (1 with young) October 7, 1941).

Distribution and Ecology. — *Cambarus bartoni ornatus* is distributed through the lower Kentucky River drainage and short tributaries to the Ohio above Louisville. It was encountered twice in the Salt River drainage. This headwaters species is found under stones in roomy burrows or in flowing streams though its presence in the streams seems to be in no way connected with the rearing of the young as in the case of *diogenes*. The streams mentioned in the records flow for only a short time during the spring and remain dry channels at other seasons. The species was associated with the Ordovician and Silurian clays and limestones in every case.

Differential Characters.—*Cambarus bartoni ornatus* may be distinguished from *Cambarus bartoni bartoni* and its various subspecies by the very long and narrow areola. The cephalothorax is very wide throughout and considerably depressed and the rostrum more reduced and depressed. In this respect it exceeds the characters as represented in *C. ortmanni*. The margins of the rostrum are usually straight, subparallel, and contracting into an abbreviated acumen. The antennal scales are greatly reduced and the eyes are noticeably smaller than in the other surface subspecies of *C. bartoni* in western Kentucky. The chelae are coarsely punctate above and below with five or six low squamose tubercles on the inner margin of the palm. The fingers are not gaping and are not costate or bearded. The inner fleshy tip of the male, form I, gonopod is bulbous with an acute tip and the annulus is nearly circular.

Measurements of the type specimens are:—

	I	II	F
Total length	63.0 mm.	54.1 mm.	59.5 mm.
Length of carapace	31.9	26.2	29.2
Length of rostrum	4.5	4.4	4.3
Length of areola	14.0	11.1	12.5
Length of right cheliped	50.5	38.2	43.5
Length of right chela	28.0	19.4	23.5
Length of inner margin of palm	8.3	5.4	8.7
Length of movable finger	18.0	12.6	14.3
Length of abdomen	31.1	27.9	30.3
Width of carapace	17.0	13.1	15.3
Width of base of rostrum	4.0	3.5	4.0
Width of areola	1.4	1.4	1.3
Width of right chela	11.5	7.2	10.3
Width of 2nd abdominal segment	13.9	11.8	13.5

Type specimens have come from Ellis Branch, 4 mi. w. of Carrollton, Carroll County, Kentucky. The holotype, male, form I, is U.S.N.M., No. 81330; the allotype, male, form II, is U.S.N.M., No. 81331; and the allotype, female, is U.S.N.M., No. 81332. Paratypes from Ellis Branch and Hardy Creek are deposited in the Museum of Comparative Zoology. Para-

types from the head of Drennon Creek are in the Museum of Zoology, University of Michigan, and the paratypes in the collection of the writer are from a tributary to Severn Creek, Owen County.

Affinities.—The species is probably the climax of a series of varieties of *C. b. striatus* in western Kentucky. The series seems to run: *striatus*-Barren River *striatus-tenebrosus-ornatus*. There is a question as to whether the latter two should be reversed for *ornatus* may be the parent species of *tenebrosus* and thus would tend to substantiate the theory for the preadaptation for cave life. However, I arrange my series as above because surface characters seem to be superimposed upon cave modifications. The carapace is wide throughout and yet the cylindrical tendency usually accompanying the robustness has been replaced by considerable depression which may reach the extent of apparent concavity along the areola. The eyes are reduced as in *tenebrosus*, yet the species does not inhabit cave waters nor is it an habitual burrower. Furthermore, the color in life is a conspicuous pattern of dark olive-green on a ground color of light gray-green. This represents excessive development of the persisting green undercolor and a total atrophy of the brown pigment of *tenebrosus*.

CAMBARUS ORTMANNI Williamson (1907)

Distribution and Ecology.—*Cambarus ortmanni*, an addition to the state list, was previously known only from Wells County, Indiana, and Cincinnati, Ohio. In Kentucky the species has been encountered in the Salt, Kentucky, and Licking drainages. The specimens were mostly taken from burrows around large stones on the margins of the streams. Smaller specimens were found in the fast water of the riffles of these streams.

Taxonomic Remarks.—The spines of the carpus are obtuse in the Kentucky specimens in contrast to the knob-like characters of the Wabash specimens. The subquadrangular, robust carapace is evident and the cephalothorax is markedly longer than the abdomen as described by Williamson. In addition, the species can be distinguished from *laevis* in the southern part of the range by the longer, narrower areola. The areola is not quite so long and much narrower than in *C. b. ornatus*. The female has a more circular annulus which suggests closer relationship with the *diogenes* section. The fleshy tip of the gonopod in the male, form I, has a hump on the dorsal side and the fleshy tip is joined to the shank at a 45° angle as stated by Williamson. He suggests that *C. ortmanni* might be related to *C. carolinus* and *C. monongalensis*. However, the tendency of *C. b. laevis* in the valley above the Falls of the Ohio preludes the species *ortmanni*.

CAMBARUS DIOGENES Girard (1852)

Distribution and Ecology.—*Cambarus diogenes* has been found in most of the major drainages of Kentucky. It is quite possible that this burrower will be found in every county of the commonwealth. The species is abundant

in the sandy and muddy stream margins of western Kentucky. It is common in the flood plains of the rivers in the east. There is a section of "slough country" in the Tygart and Little Sandy bottoms in Boyd and Greenup counties where the species is very abundant.

Taxonomic Remarks.—The most striking variation among my Kentucky material of this species occurs in a specimen from Cumberland County. The rostrum has straight sides strongly converging to the tip to form a sharp triangle. It does not seem to be an injured specimen with a regenerated rostrum such as occurs frequently among the stream crayfishes. The areola of the eastern variety is not entirely obsolete especially anteriorly. The *diogenes* from western Kentucky possess a totally obsolete areola. The rostrum of the western variety is deeply excavated in contrast with the subplane rostrum of the eastern specimens. The eggs of all the "berried" females collected were jet black in life.

Doubtful, or Otherwise Spurious Records

ORCONECTES SLOANI (Bundy) (1876)

This species has been reported from Kentucky by Bundy (1876:24), however, he may have assumed that the distribution extended south of the river since his type locality was at New Albany, Floyd County, Indiana. Repeated search in the Louisville area has failed to disclose the presence of the species in Kentucky. I have pointed out (1941:95) that large streams seem to act as barriers to *O. sloani*. Accordingly, this species might be confined to southeastern Indiana and southwestern Ohio. The Ohio River deserves considerable study from the standpoint of the crayfishes. The eastern species occurs about fifty miles farther downstream than the limit of the range in the tributary streams. Below the Falls of the Ohio the whole ecology changes and the species of the sluggish prairie streams have come eastward. The prevailing species of the area are considerably complicated by this pressure. Until specimens of *O. sloani* are taken in Kentucky the species should remain on the doubtful list for the state.

CAMBARUS LONGULUS LONGIROSTRIS (Faxon) (1885)

There are three specimens in the Museum of Comparative Zoology (M.C.Z., No. 3628) from "Cumberland Gap, Kentucky," collected by Walter Faxon in 1874. Ortmann collected in the vicinity of Cumberland Gap in 1913 and he referred to this record as "Cumberland Gap, Claiborne Co., Tennessee. (Faxon) (probably in Indian Creek)." (Ortmann 1931:121). I was not able to collect the species in Kentucky and, accordingly, the species is omitted from my list.

Aside from possible new species it is likely that the following species will be found to occur within the state: *Orconectes palmeri, Cambarus montanus montanus,* and *Cambarus carolinensis*.

REFERENCES

ACADEMY OF NATURAL SCIENCES OF PHILADELPHIA. 1843—Stated Meeting, May 24, 1842. Vice President Morton in the Chair. Proc. Acad. Nat. Sci. Phila. **1**:174-175.

COPE, EDWARD DRINKER. 1872—On Wyandotte Cave and its Fauna. Amer. Nat. **6**(7):406-422, 8 fig.—Reprinted in: Third and Fourth Ann. Repts. Geol. Sur. Ind. (for 1871-1872), pp. 157-182, 8 fig.—Reprinted in part: Eighth, Ninth, and Tenth Ann. Repts. Geol. Sur. Ind. (for 1876-1878), pp. 489-506, 8 fig.

CREASER, EDWIN PHILLIP. 1933—Description of Some New and Poorly Known Species of North American Crayfishes. Occas. Pap. Mus. Zool. Univ. Mich. **275**:1-21, 2 pls.

ERICHSON, WILHELM FERDINAND. 1846—Uebersicht der Arten der Gattung Astacus. Arch. f. Naturg. **12**(1):86-103.

———1846—Nachtrag zur Uebersicht der Gattung Astacus. Arch. f. Naturg. **12**(1): 375-377.

FORBES, STEPHAN ALFRED. 1876—List of Illinois Crustacea, with Description of New Species. Bull. Ill. Mus. Nat. Hist. **1**:3-25.

GIRARD, CHARLES FREDERIC. 1852—A Revision of the North American Astaci, with Observations on their Habits and Geographical Distribution. Proc. Acad. Nat. Sci. Phila. **6**:87-91.

GOODNIGHT, CLARENCE JAMES. 1940—Rediscovery of Cambarus compressus Faxon in Mississippi. Amer. Midl. Nat. **23**(1):222-223.

HAGEN, HERMANN AUGUST. 1870—Monograph of the North American Astacidae. Ill. Cat. Mus. Comp. Zool., No. III, pp. 1-109, 11 pls.

HAY, WILLIAM PERRY. 1893—Observations on the Blind Crayfishes of Indiana, with a Description of a New Subspecies: *Cambarus pellucidus testii*. Proc. U. S. Nat. Mus. **16**(935):283-286, 2 pls.

———1902—Observations on the Crustacean Fauna of the Region about the Mammoth Cave, Kentucky. Proc. U. S. Nat. Mus. **25**(1285):223-236, 1 fig.

———1902—Observations on the Crustacean Fauna of Nickajack Cave, Tennessee, and Vicinity. Proc. U. S. Nat. Mus. **25**(1292):417-439, 10 figs., 1 map.

HOBBS, HORTON HOLCOMBE, JR. 1942—A Generic Revision of the Crayfishes of the Subfamily Cambarinae (Decapoda, Astacidae) with the Description of a New Genus and Species. Amer. Midl. Nat. **28**(2):334-357, 3 pls.

HOBBS, HORTON HOLCOMBE, JR. AND CHARLES SAMUEL SHOUP. 1942—On the Crayfishes Collected from the Big South Fork of the Cumberland River in Tennessee During the Summer of 1938. Amer. Midl. Nat. **28**(3):634-644, 1 fig., 1 pl., 1 table.

HUNTSMAN, ARCHIBALD GOWANLOCH. 1917—Concerning Some Ontario Crayfishes. The Ottawa Nat. **30**(10):130-132.

HUXLEY, THOMAS HENRY. 1878—On Classification and Distribution of Crayfishes. Proc. Zool. Soc. London: 752-788, with woodcuts.

ORTMANN, ARNOLD EDWARD. 1931—Crawfishes of the Southern Appalachians and the Cumberland Plateau. Ann. Carnegie Mus. **20**(2):61-160.

PACKARD, ALPHAEUS SPRING, JR. 1886—The Cave Fauna of North America, with Remarks on the Anatomy of the Brain and the Origin of the Blind Species. Mem. Nat. Acad. Sci. **2**:1-156, 20 figs., 2 maps, 27 pls.

PARK, ORLANDO, TILDEN WIRT ROBERTS, AND STANLEY [CYRIL] HARRIS.* 1941—Preliminary Analysis of Activity of the Cave Crayfish, *Cambarus pellucidus*. Amer. Nat. **75**:154-171, 5 figs., 3 tables.

RAFINESQUE, CONSTANTINE SAMUEL. 1817—Synopsis of Four New Genera and Ten New Species of Crustacea, found in United States. Amer. Monthly Mag. & Crit. Rev. **2**, Art 7(9):40-43.

RHOADES, RENDELL. 1941—The Distribution of *Cambarus sloani* Bundy, in Ohio. Ohio Journ. Sci. **41**(2):93-98, 7 figs., 1 map.

———1941—Notes on Some Crayfishes from Alabama Caves, with the Description of a New Species and a New Subspecies. Proc. U. S. Nat. Mus. **91**(3129): 141-148, 2 figs.

SHULL, CHARLES ALBERT. 1909—Some Abnormalities and Regeneration of the Pleiopods of Cambarus and other Decapoda. Biol. Bull. **16**:297-312, 1 pl.

TELLKAMPF, THEODOR G. 1844—Ueber den blinden Fisch der Mammuth-höhle in Kentucky, mit Bemerkungen über einige andere in dieser Höhle lebende Thiere. (Taf. IX). Arch. f. Anat. Physiol. u. wissens. Med., herausg. von Dr. Johannes Müller. **1844**:381-394.—Reprinted in (English): N. Y. Journ. Med. and collateral Sci. **1845**(July):84-93, 1 pl.

WILLIAMSON, EDWARD BRUCE. 1905—Odonata, Astacidae, and Unionidae Collected along the Rockcastle River at Livingston, Kentucky. Ohio Nat. **5**(6):309-312.

———1907—Notes on the Crawfishes of Wells County, Indiana, with the Description of a New Species. Thirty-first Ann. Rept. Dept. Geol. and Nat. Res. Ind. (for 1906):749-763, 1 pl.

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* I have been informed by Dr. C. L. Turner, Department of Zoology, Northwestern University, that S. J. Harris, coauthor with Dr. Park and Mr. Roberts, is Mr. Stanley Cyril Harris.

Studies on the Flatworm Catenula virginia[1]

Egbert Heinlein and Henry E. Wachowski

Only two species of the flatworm Catenula have been reported for the United States: *Catenula lemnae* (Duges), which also occurs in Europe, and *Catenula virginia,* recently described by Kepner and Carter (1939). The latter species was discovered growing abundantly in a large aquarium in the biology laboratory at Catholic University. From this source the original cultures were prepared. Identification of the animal used in the present work as *Catenula virginia* was based on the two diagnostic characters mentioned by Kepner and Carter, viz., the presence in the cephalic lobe of a sensory dorsal pit extending along the mid-dorsal line from the tip of the cephalic lobe to a little beyond the middle of the mid-dorsal line, and secondly, the position of the statocyst against the posterior vertical wall of the cephalic ganglion rather than dorsal to it (Figs. 3, 4, 5).

Since Kepner and Carter's brief description nothing further has appeared in the literature on *Catenula virginia.* The purpose therefore of the present work is to report new data on the morphology, reproduction and nutrition of the animal, as well as to present the results of experiments dealing partly with the response of this worm to various culture media and partly with attempts to induce sexuality by altering the environment.

Morphology

Catenula virginia is characterized by the chain-like union of two or more zooids into a single specimen. The body of each zooid is spindle-shaped, approximately 0.5 mm. long, and divided into an anterior cephalic lobe bearing a statocyst, and the posterior body proper. The two regions are separated by a conspicuous transverse groove.

The general morphological features of *C. virginia* are shown in Figs. 1, 6, 8, and 9. The body of the animal is divisible into three clearly distinguishable main tissues. The outermost is a low epithelium, uniformly ciliated except for the transverse groove, where the cilia are larger. In specimens stained by the Feulgen method the epithelial nuclei appear as evenly staining, more or less spherical bodies, about 1.5μ in diameter. The middle layer of tissue, making up the bulk of the body, consists of mesenchyme which is differentiated into an axial, coarsely granular region and a peripheral region of large, radiating, vacuolated cells. Vital staining with neutral red, methylene blue and Nile

1 A contribution from the Department of Biology, the Catholic University of America, Washington, D.C. This paper, prepared under the direction of Dr. E. G. Reinhard, is based on the authors' dissertations submitted in partial fulfillment of the requirements for the degree of Master of Science. The authors wish to express their sincere gratitude to Doctors Reinhard and T. von Brand for their valuable help in the work on *C. virginia.*

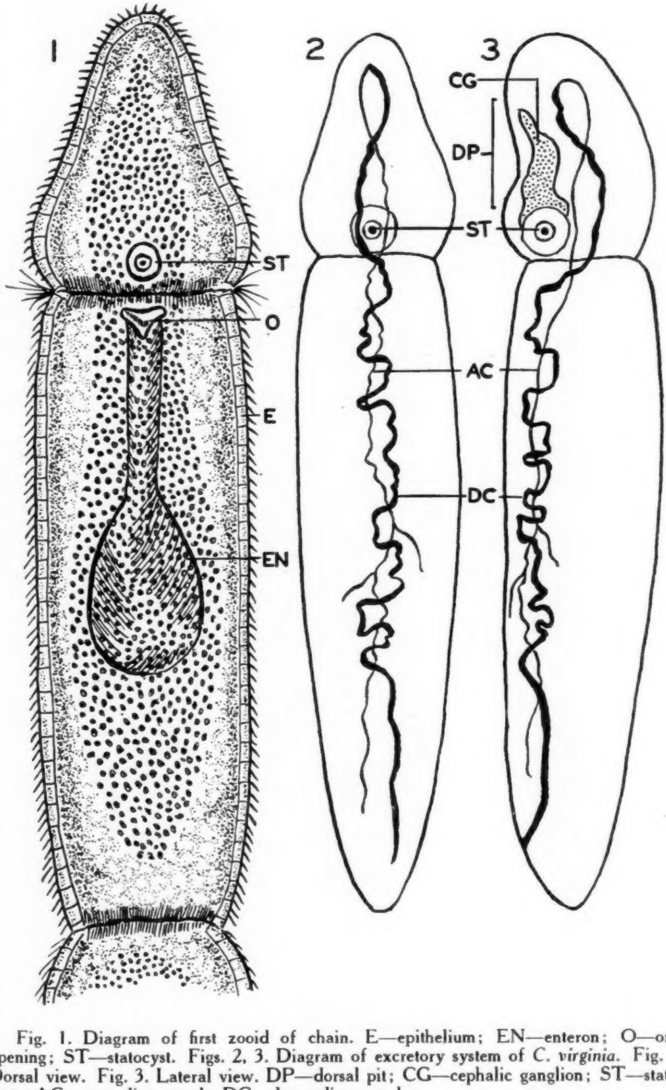

Fig. 1. Diagram of first zooid of chain. E—epithelium; EN—enteron; O—oral opening; ST—statocyst. Figs. 2, 3. Diagram of excretory system of C. *virginia.* Fig. 2. Dorsal view. Fig. 3. Lateral view. DP—dorsal pit; CG—cephalic ganglion; ST—statocyst; AC—ascending canal; DC—descending canal.

blue revealed cells of irregular shape scattered throughout the mesenchyme, being especially numerous around the oral opening. These are probably identical with the neutral red atrocytes described for Stenostomum by Westblad (1930) who attributes an excretory function to them. The nuclei of the mesenchymal layer are somewhat larger than those of the epithelium, measuring 1.9μ to 2.5μ in diameter. They vary in shape from oval to rod-shaped structures. The mesenchymal nuclei show small chromatin granules which give them a stippled appearance. The third tissue, the entoderm, constitutes the lining of the enteron. The entoderm is similar in appearance to the outer epithelial layer. It consists of a layer of low, ciliated cells.

The alimentary canal presents a T to Y-shaped oral opening on the ventral side, immediately posterior to the transverse groove. The mouth is continuous with a highly ciliated pharynx, which in turn opens into the sac-like enteron. The enteron usually contains a large food bolus which is constantly kept in motion by the action of the cilia lining the enteron. The enteron extends slightly beyond the middle of the body.

The cephalic lobe is characterized by the presence of the statocyst, sensory

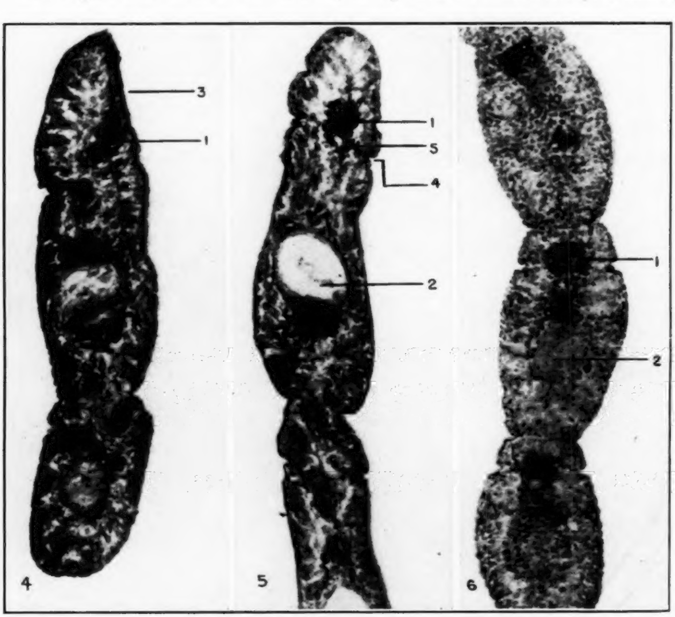

Fig. 4. Lateral view of animal with second zooid just forming. Sagittal section. ×237. Fig. 5. Horizontal longitudinal section of chain of two zooids. ×237. Fig. 6. Whole mount stained by Feulgen method. 1—cephalic ganglion; 2—enteron; 3—dorsal pit; 4—transverse groove; 5—statocyst sac.

dorsal pit, and cephalic ganglion situated with respect to each other as outlined above. Stained by the Feulgen method the nuclei of the ganglion appear as small, elongate and intensely staining bodies arranged as a compact, bulb-like mass. Beneath the statocyst sac and encircling the esophagus, the same staining technique reveals a funnel-shaped ring of nuclei identical in shape and staining intensity with the nuclei of the ganglion, indicating possibly the presence of an esophageal nerve ring.

The excretory system is protonephridial. It is made up of a double coiled canal, and lies along the mid-dorsal line. The system starts as an ascending canal near the posterior end of the body, gives off several small branches, forms a loop in the cephalic lobe, and continues downward towards the posterior as the descending canal, terminating in a pore slightly beyond the point of origin. The section posterior to the transverse groove is dorsal in position, while in the cephalic lobe the canal lies closer to the ventral surface of the animal. The excretory system is diagrammed in Figs. 2 and 3.

Experiments with Culture Methods

The stock culture medium was prepared according to the method recommended for Catenulidae by J. W. Nuttycombe (1937). It is essentially an infusion prepared by boiling 200 to 300 grains of seed wheat in 250 cc. of spring water. The addition of several small calcium carbonate chips to each culture dish helps to establish some control of the pH of the medium. In this medium the Catenulae have now been cultured for over two years; they thrive well and need but little attention.

It seemed desirable, however, to seek a more standard, more rigidly controlled medium. Since little information on such cultures for the Turbellaria was available, the compilations of protozoan culture media of Hall (1937) and Trager (1937) were used as a guide. Media of the tryptone and peptone type were tried in concentrations varying from 3.0% to 0.5%. None of these proved suitable for the growth and development of the worm. Media of liver extract, yeast extract, and combinations of these were hardly more promising. A medium prepared from Pablum was successful, except that it seemed to foster the growth of mold more than did the wheat grain infusion.

During experiments with culture methods the apparent adaptability of *Catenula virginia* to concentrations of tryptone that ordinarily proved fatal was observed. The tryptone medium used in these experiments was made up according to the following formula:

Difco tryptone	1.0 gram
0.4% NaCl solution to make	1000 cc.

The worms were transferred from the stock culture to a medium composed of 9 parts Pablum to 1 part tryptone medium. They were then transferred at three day intervals to media in which the proportion of tryptone was gradually increased. The results are given in the following table:

TABLE 1

Transfers	Results
to 9-1 Pablum tryptone Wheat grain infusion	normal activity
to 8-2 Pablum tryptone	normal activity
to 7-3 Pablum tryptone	slight loss of activity
to 6-4 Pablum tryptone	
to 5-5 Pablum tryptone	gradually increasing loss of activity
to 4-6 Pablum tryptone	
to 3-7 Pablum tryptone	inactive
to 2-8 Pablum tryptone	rapid death
Wheat grain infusion to 5-5 Pablum tryptone	rapid death

Transfer of the Catenulae directly from the stock culture to the 5 part Pablum-5 part tryptone medium invariably resulted in death. Repetition of the graduated series of media with longer time intervals between transfers failed to give worms that would survive beyond the 3 part Pablum-7 part tryptone medium. The apparent adaptation of Catenulae to ordinarily toxic concentrations of tryptone resembles the adaptation to poisons reported for some protozoan forms.

Attempts were likewise made to obtain sterile cultures. Sterilization was effected by combining the methods described by Glaser and Coria (1930) with those of Hetherington (1934). The method of Glaser and Coria is based on the geotropic movement of the organisms through a column of sterile liquid. The Catenulae, which are positively geotropic, were therefore introduced into the top of a 14-inch glass tube filled with sterile Pablum medium. After an hour the sealed bottom end of the tube was broken carefully into a dish of sterile medium, and the washing method of Hetherington then used. After seven washings a sterile culture of Catenula was obtained. The sterility of the culture was established by negative agar slants taken immediately after sterilization and after a 24-hour interval, and kept at both room temperature and at 35° C. Stained smears of the culture also proved negative. The behavior of the Catenulae in the sterile culture was apparently normal for 24 hours, but then movement and activity of the worms decreased, they appeared somewhat contracted, and death of the culutre followed in 48

hours. Subsequent sterile cultures in Pablum as well as in sterile wheat grain infusion met with the same fate.

Reproduction

Asexual reproduction in *Catenula virginia* takes place by transverse fission of the type known as paratomy, which results in chain formation. The division into zooids in the chain follows a definite and regular rhythm and pattern, very similar to that described for Stenostomum by Child (1902).

Sexual reproduction in the family Catenulidae is generally reported as being protandrically hermaphroditic. According to Bresslau (1933), sexually mature animals might be expected to make their appearance in the fall. How-

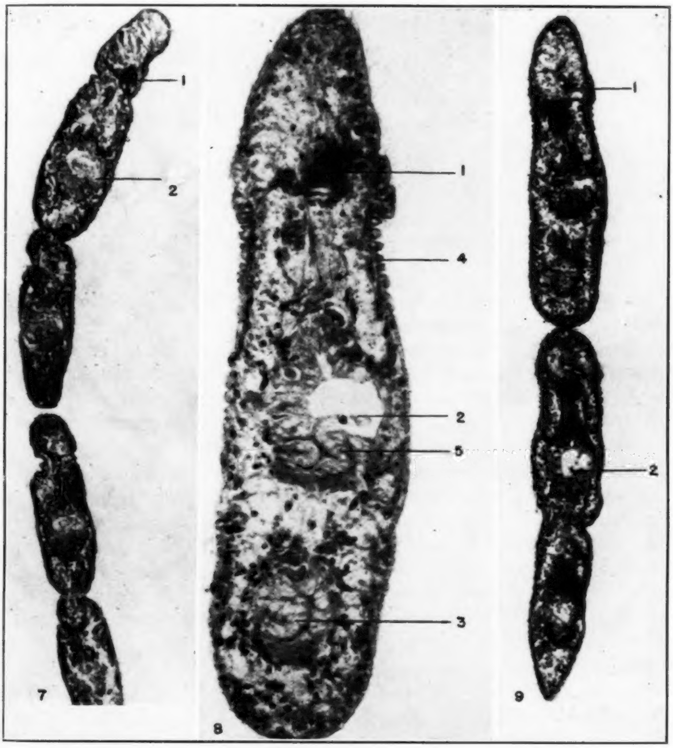

Fig. 7. Horizontal longitudinal section of chain of 4 zooids. ×120. Fig. 8. Horizontal longitudinal section of chain of two zooids, with second just forming. ×405. Fig. 9. Horizontal longitudinal section of chain of 4 zooids. ×218. 1—cephalic ganglion; 2—enteron; 3—enteron of second zooid; 4—epithelium; 5—lining of enteron.

ever, sexual reproduction has never been established for the genus Catenula. Regular examinations of the eight *C. virginia* cultures over a period of almost two years has yielded no evidence of sexual reproduction. Attempts therefore were made to induce sexual maturity experimentally. Hyman (1941) succeeded in inducing the sexual phase in a planarian by lowering the temperature to 15° C. for two weeks or less, then raising it to approximately 25° C. Van Cleave (1929) attempted without success to induce sexuality in a species of Stenostomum by over-feeding, and temperate variation.

In the course of the present work on *C. virginia* the method of Hyman was first tried. The Catenulae were kept at 17° C. for a week, then kept at 25° C. for a day before examination. Examination revealed that all the worms had been killed off and had disintegrated. The experiment was repeated, but this time exposure to cold was allowed for only three days. Immediate examination showed that most had disintegrated, but a few had survived. These were inactive, however, and after two days at 25° C. showed curious deformations, with a marked swelling of the first zooid. The cause of the swelling was not apparent. No trace of new development could be found and after four days the worms had returned to their normal form. A third exposure to cold, this time for four days, resulted in the disintegration of the entire culture. It was then thought that perhaps a rapid freezing might provide the shock or stimulus to induce changes in the Catenulae. Accordingly, a few Catenulae were placed in a drop of water on a coverslip and frozen rapidly on the bed of a freezing microtome. The worms were killed by this action but did not disintegrate.

Growing the Catenulae in a medium where the food supply was kept especially plentiful gave a luxuriant culture of worms somewhat larger in size than those of the stock culture, but three months in such a medium failed to give any indication of sexual development. Starvation produced thin, sluggish worms, with a few aberrant forms resembling those reported for Stenostomum by Van Cleave (1929). Return to a normal medium gave normal worms with no sexual development.

Working then on the premise that possibly the sexual phase had escaped detection under normal observation, and that eggs had perhaps been deposited in the cultures, all the Catenulae were removed from an old culture in late October, the cultures filtered, the collected debris placd in another culture dish, and fresh water added to it. Fresh Catenulae had likewise been placed in the filtrate of the old culture. Up to the following March no Catenulae were found in the former, nor had any change been observed in those that had been introduced into the filtrate of the old culture.

Finally, the worms were stained by the Feulgen method in the hope of revealing testicular tissue. The staining was performed both with whole specimens and with sections, but no gonadal tissues were detected.

Feeding Habits and Behavior Characteristics

According to Westblad (1922), Turbellaria feed in general on small animals such as rotifers, copepods, cladocera, infusoria and others. Although

amoebae, paramecia, daphniae and ostracoda were at certain times present in great numbers in the culture media, Catenula was never observed to prey on these. A careful inspection of many specimens never revealed traces of ingested animals of any sort in the digestive tract of the flatworm.

In the stock cultures the Catenulae were observed crowded around the wheat grains. Whether they fed on the decomposing particles directly, or on the bacteria growing on the wheat could not be definitely established.

Kepner and Carter observed that their Catenulae fed on a decaying snail. In order to check this, a number of Catenulae were placed in a watch glass containing a piece of dead and decomposing snail. It was noted that the worms stayed within the immediate vicinity of the snail and lived on it for a period of four weeks, by which time the piece of snail had disappeared.

On the basis of these observations it would seem that Catenula lives on decaying organic material rather than on living animals.

The ejection of indigestible material takes place through the pharynx and oral opening. The peculiar fact was noted that all members of the chain defecated at almost the same moment. First it was thought that this was due to the pressure of the coverslip, but later the same phenomenon was watched without a coverslip.

A peculiar tendency of Catenula to mass into almost solid colonies in the culture was observed. For several days the Catenulae will travel about normally in culture, then the worms will gather without apparent cause under one or the other of the calcium carbonate chips, forming an almost solid mass there. Adding to the strangeness of this condition is the fact that the Catenulae will all gather under one such chip, while another, a short distance removed from the first, will have no Catenulae under it. A further manifestation of this phenomenon is the congregation of the Catenulae also in the open. Occasionally among the debris at the bottom of the culture round, brownish masses, ranging from 2 to 5 mm. in diameter were observed. These proved to be Catenulae, intertwined intricately, and exhibiting a writhing motion. At intervals of about a minute these solid masses contracted in toto. Upon exposure to strong light the individual Catenulae would rapidly begin to free themselves from the colony and travel away from the light. A somewhat similar observation was reported by Minnich (1941) for a marine tubificid worm, *Clitellio arenaria* (O. F. Müller), except that in this case the response to light was the opposite; the worms contracted into a more compact mass instead of breaking away.

Likewise observed was the response of individual worms to what apparently was unfavorable environment. In two of the cultures several worms were noted coiled into a spherical form in which the individual zooids were hardly distinguishable except for their statocysts. The position of the statocysts indicated that the zooids had "folded" so that the posterior end of the last zooid rested against the head of the first. Nothing like a cyst wall could be detected, and transfer to fresh medium caused the worms to assume their normal form.

Note on Killing and Fixation

Considerable difficulty was encountered in early attempts at fixation. Many of the reagents tried tended to distort the tissues by causing the worms to swell as well as to adhere to the bottom of the watch glass or to the walls of the pipette. After considerable experimentation Flemming's "strong" solution proved most satisfactory.

In normal life Catenula reacts to stimuli by prompt and vigorous contraction. It is therefore difficult to kill the animal in a perfectly expanded condition. Both hot and cold killing fluid were employed; ordinary anesthetizing agents such as chloroform, chloretone and magnesium sulphate were of little avail; resort was finally had to cold. Before killing, the worms were placed in the refrigerator and exposed to cold for about fifteen minutes. The action of the cold rendered them insensitive to the killing fluid, leaving them in an expanded condition.

Summary

The general morphology of the flatworm *Catenula virginia* is outlined and observations on feeding habits and behavior characteristics are noted.

Experimental work on culture media revealed that media made with Pablum will give successful cultures of the worm. More standardized media of tryptones, peptone, yeast extract and liver extract were found to be unsuitable for the growth of Catenula, although the worm did show some adaptability to a combined Pablum-tryptone medium. Sterile cultures failed to support the growth of Catenula for more than 24 hours.

Sexual maturity was neither observed nor induced experimentally through environmental changes during the two year period covered by the present paper.

REFERENCES

Bresslau, E. 1933—*In:* Kükenthal, W., Handbuch der Zoologie, 2. Band: Vermes Amera, Vermes Polymera, Echiurida, Sipunculida, Priapulida. Part 1, pp. 1-300. Berlin and Leipzig, 1933.

Glaser, R. W. and N. A. Coria. 1930—Methods for the Pure Culture of Certain Protozoa. J. Exper. Med. **51**:787.

Hall, R. P. 1937—Growth of Free-living Protozoa in Pure Cultures. *In:* Galtsoff et al., Culture Methods for Invertebrate Animals, p. 51. New York, 1937.

Hetherington, A. 1934—The Sterilization of Protozoa. Biol. Bull. **67**:315.

Hyman, L. H. 1941—Environmental Control of Sexual Reproduction in a Planarian. Anat. Rec. **81**:108. Suppl.

Kepner, W. A. and J. S. Carter. 1930—Catenula virginia n. sp. Zool. Anz. **91**:300.

Minnich, D. E. 1941—The Light Response of the Marine Tubificid Worm Clitellio arenarius (O. F. Müller). Jour. Exp. Zool. **87**:397.

Nuttycombe, J. W. 1937—Wheat-grain Infusion. *In:* Galtsoff et al., Culture Methods for Invertebrate Animals, p. 135. New York.

Trager, W. 1937—Some Methods for the Pure Culture of Protozoa. *In:* Galtsoff et al., Culture Methods for Invertebrate Animals, p. 112. New York.

Van Cleave, C. D. 1929—An Experimental Study of Fission and Reconstitution in Stenostomum. Physiol. Zool. **2**:49.

Westblad, E. 1922—Zur Physiologie der Turbellarien. Lunds Universitets Årsskrift NF. Avd. 2, **18**.

Some Effects of Flooding and Waterfowl Concentration on Mammals of a Refuge Area in Central Illinois

Lee E. Yeager and Harry G. Anderson

The Lake Chautauqua National Wildlife Refuge, administered by the U. S. Fish and Wildlife Service, is a leveed, bottomland lake in Mason County, about five miles upstream from Havana, Illinois. It is east of and lies parallel to the Illinois River. About 85 per cent, or 4,250 acres, of the total refuge area is water, the level of which is maintained by nine miles of dikes and a system of locks and dams. Chautauqua Lake, formerly a drainage district, was cultivated 1924-26, inclusive. In 1927 breaks in the levee returned the area to a series of lakes with fluctuating levels, a condition prevailing until 1936 when the refuge was established. The 5,000-acre area is now one of the most important duck concentration grounds on the Mississippi flyway.

Opportunity to make the observations recorded here was afforded by the proximity of the Chautauqua Refuge to other field projects. Many of the observations were made in connection with these projects, and all of them were taken personally by the writers, either alone or working in company.

In connection with this work we wish to thank Mr. Homer L. Bradley, Refuge Manager, for his courtesy and assistance. Helpful suggestions were received from Mr. Frank Bellrose, Dr. Jessop B. Low, and Dr. Wilfred D. Crabb, all of whom read the manuscript. Mr. C. S. Spooner, Jr., made the drawing for Fig. 1.

As indicated by the title, this paper considers mammal behavior under atypical conditions, although the reactions described are probably consistent with behavior resulting from such circumstances as prevailed at the time of the study. The two main atypical conditions were flooding and the presence of hundreds of thousands of ducks during the fall and winter. The ducks, particularly during the hunting season, provided, in the form of cripples and unretrieved kills, an abundance of food for carnivorous species. Both flooding and food abundance, therefore, further concentrated these populations, the former affecting woodchucks and cottontail rabbits particularly, and the latter raccoons and minks. Of opossums, it seems probable that both conditions contributed to their unusual density on the levee.

The fact that the refuge has offered full protection to all species since its establishment in 1936 is profoundly important in accounting for the large resident population of mammals thereon previous to the time of this study.

The Levee Habitat

Practically all data presented in this article were taken on the Chautauqua Refuge levee, over a distance of about six miles. This embankment varies from 15 to 20 feet in height. Its width on top averages about 12 feet, but ranges from five or six to perhaps 40 feet, and is not uniformly level. The base width averages about 100 feet. At many points the side slopes are steep. In age, the levee varies from two to about 20 years, the newest part, less than three miles in length, having been built higher since 1939. In this case, loose sand was mainly used as fill; the older parts of the levee are varying mixtures of sandy clay. About seven miles of the levee are bordered on both sides by water, which, on the outside, is mainly the channel excavated for fill.

Vegetation on the levee proper varies from weeds and grass along the newest part, to 24-inch cottonwood trees along the oldest part. Adjacent vegetation on the land-bordered sections consists of marsh, willow thickets, young river-bottom forest, a hardwood ridge, and a 120-acre stand of overmature river-bottom timber on the refuge for a distance of three-quarters of a mile. The physical and vegetational characteristic of the levee area are shown in Fig. 1. On the basis of soil and plant life it is possible to divide the levee into zones, as given in Table 1.

TABLE 1.—Soil-cover zones along the Chautauqua National Wildlife Refuge levee and adjacent area.

Soil	Length, Miles	Vegetation			Water at normal stage, Miles*	
		Levee	Adjacent to Levee		Refuge Side	Out-side
			Refuge side	Outside		
Loose Sand	3.00	Weeds and millet on top and under slopes; small willows at foot of slopes.	River bottom forest, sapling stage; 1 mile.	No bordering vegetation	2.00	3.00
Clay	2.75	Weeds, sweetclover and vines on top; willows and cottonwoods up to 10-inch diameter on slopes.	River bottom forest, sapling-small tree stage; 0.5 mile.	No bordering vegetation; marsh-willow flat beyond dredge ditch; 1.75 miles.	2.25	2.75
Clay	.75	Weeds, sweetclover, and vines on top; willows and cottonwoods up to 25-inch diameter on slopes.	Mature river bottom forest; 0.75 mile.	No bordering vegetation; narrow strip of riverbottom forest beyond dredge ditch.	No water	.75

* Quiver Creek and ditch excavated for levee fill counted as water where they border levee. Average width of each is about 60 feet.

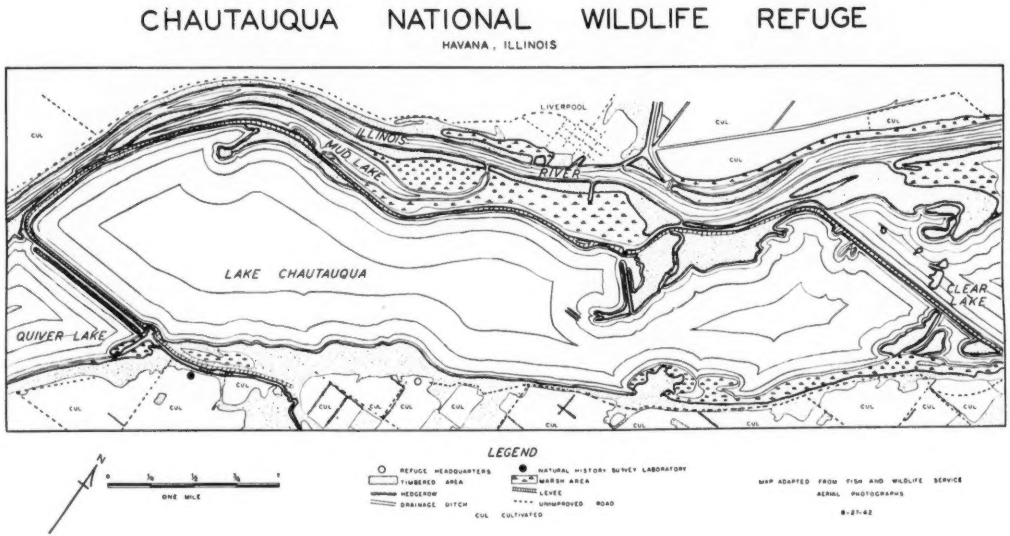

Fig. 1.—Map of Lake Chautauqua National Wildlife Refuge and vicinity, Havana, Illinois.

Effects of Flooding

The height and duration of the two floods that inundated the refuge in October and November, 1941, and February, 1942, are presented graphically in Fig. 2. In this chart the average temperature is given for the period of October-February, inclusive. All data are summarized by five-day intervals.

The most pronounced effects of flooding related to population density, denning, and certain other behavior. There was clearly a differential effect by species, ranging from heavy mortality in the case of woodchucks to apparently little basic change in the behavior of minks. In addition to these two species, observations were also made on fox squirrels, cottontail rabbits, raccoons, opossums, muskrats, red foxes, and feral dogs. Only very general notes were gathered on mice, shrews, and moles.

Population Density and Ground Dens

It is unfortunate that the various levee populations could not be censused precisely, either under normal or flood conditions. There are no completely satisfactory techniques for such measurements. On basis of the evidence at hand, it seems safe to state that raccoons, opossums, woodchucks, and cottontail rabbits, at least, were present in concentration numbers, particularly during the flood periods. It was not possible to determine the concentrating effect of

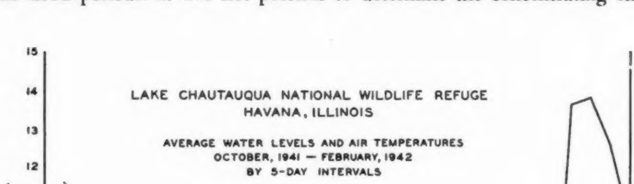

Fig. 2.—Average water levels and air temperatures, October, 1941—February, 1942, at Lake Chautauqua National Wildlife Refuge, Havana, Illinois.

flooding, if any, on squirrels; muskrats were too aquatic and red foxes were too low in numbers to permit conclusions. Presumably mice, moles, and shrews were forced to higher ground.

The observed density of dens and populations on the levee was not due wholly to flooding. Appreciable mammal populations were resident there before October, 1941. At the time of flooding, the levee was the only exposed land in the refuge vicinity; and at all times, due to the high water table characterizing adjacent low areas, it offers the best site for ground dens.

Immediately following the first flood peak, October 10-15, an unusual amount of den construction was apparent. Noticeable also was the concentration of cottontail rabbits and the conspicuous enlargement of game trails, many of which were used so much that even individual raccoons could not be followed in the mud medium.

The usual difficulty in determining den use was encountered. Inspections under conditions of both mud and snow failed in some cases to reveal specific occupancy, or whether more than one species was present. Aiding in making the final decisions were live trapping, the excavation of a few shallow dens at points where they endangered the levee, the size of den openings, and the presence of hair, tracks, and other signs about the entrance. Not eliminated in every instance were dens receiving only part-time use, use by more than one species, and abandonment due to the rising water table. During the course of the winter changes were noted in the use of dens, such as succession of species, desertion, or reconditioning of cavities.

Throughout the study the writers tried to be conservative in evaluating den use. At times the tracks of two or more species led into and out of the dens. Such cavities, where use was obviously habitual, were listed under the species showing the greatest total evidence of habitation. Rabbit use was discounted except where pronounced. Instances in which mink tracks led to dens with large openings, or where the evidence showed that any animal merely entered and left a den, were discarded. Only dens with smoothly worn entrances and connected with fresh trails were counted in the tabulations.

Table 2 gives the number and density of ground dens and their association with soil and cover as to occupancy, age and position on the levee. Particularly noticeable was the scarcity of dens in loose sand, for which the unstable nature of the soil and relative isolation of much of this levee from forest cover are largely responsible. One-third of the sand-levee dens were not in use, and all of these were caved-in and obviously uninhabitable without repairs. In the forest-bordered clay type, where by far the greatest density was found, 42 per cent of the dens apparently were unused, but here ground cavities remain usable over long periods. Only 9 per cent of the dens in the small-timber bordered levee, also of sandy clay, were unused, a condition probably due to an outward push of overcrowded populations along the three-fourths mile of levee bordered by the over-mature riverbottom stand.

TABLE 2.—Density, occupancy, age, and position of ground dens on Chautauqua National Wildlife Refuge levee, Havana, Illinois, fall and winter, 1941-42.

Soil	Adjacent Cover	Length of type, Miles	Number of dens	Den density per Mile	Number of Dens						Per Cent of Dens*					
					Occupancy		Age		Position on Levee		Occupancy		Age		Position on Levee	
					In Use	Not in Use	New	Old	Top	Side	In Use	Not in Use	New	Old	Top	Side
Loose sand	Weeds; willows and cottonwoods up to 10″ diameter in strip along levee	3.00	15	5.0	10	5	9	6	2	13	67	33	60	40	13	87
Clay	Willows and cottonwoods up to 24″ diameter in strip along levee	2.75	35	12.7	32	3	19	16	12	23	91	9	54	46	34	66
Clay	Heavy, mature hardwood stand of 120 acres	.75	64	85.3	37	27	11	53	19†	51†	58	42	17	83	27	73
Totals and percentages			114	....	79	35	39	75	33	87	69	31	66	34	65	35

* Percentage calculations to nearest whole number.

† Six dens in this type with top and side entrances; such dens are counted in each class, under "Position," giving a total of 120 instead of 114 dens.

That population pressure was heavy along this three-fourths mile of levee, and that some dispersal occurred, is indicated by the fact that in the loose sand and small-timbered bordered sections 67 and 91 per cent, respectively, of the dens were in active use, and 60 and 54 per cent, respectively, were new. This may be compared to the occupancy of 58 per cent, and recent construction of only 17 per cent, of the dens on the forest-bordered levee. It thus appears that the latter area was crowded nearly to capacity before flooding and that further concentration due to flooding was relieved by migration to less attractive but less densely populated levee on either side of the timber tract (Fig. 1).

The attractiveness of the woods-bordered levee to the species present is further indicated in Table 2 under "Den Density per Mile." Density was about seven times greater than along the small timber-bordered levee, and 17 times greater than in loose sand. These proportions are not subject to reduction by unlocated brush-hidden dens, since such cover was heavier on the forest-bordered levee than on any other section.

It is obvious that entrance to dens were far more common on the levee slopes than on top, regardless of soil and cover.

Dens with two or more used entrances were found only on the forest-levee, where the lowest density of new dens occurred. Only six such dens, or five per cent, were found. It is doubted that plural entrances are associated with den age, as the data appear to indicate. A more probable interpretation is that, due to heavy pressure, unused openings to used dens were reconditioned and inhabited as temporary retreats. It was not always determined with certainty whether seemingly plural entrances led to the same or to different dens, and a few decisions may, therefore, be in error. The number of openings to plural-entrance dens ranged from two to five.

BEHAVIOR BY SPECIES

The following specific accounts present such behavior as was observed in connection with flooding:

Fox Squirrels.—Fox squirrels occur in all timbered areas on the refuge. They may be said to be abundant and they often forage for some distance down the levee away from heavier woods. Flooding did not serve to drive squirrels out of timber stands, although inundation during the two peaks was five feet or more. Travel was arboreal or via numerous logs and debris floating on the water surface. During two cold periods in January and in February, 1942, these animals were repeatedly observed to travel through the woods on ice. They were not observed on or tracked across large, open, snow-covered ice fields. They used freely at all seasons several dozen wood duck boxes placed along the levee.

During the periods of flooding, and particularly at the time of zero temperatures in January, 1942, food must have been of some concern. During the

October, 1941, flood, unfallen pecans still were plentiful, and herbage, fruits, and other mast were available. Stores or caches, if in trees or other places above flood stage, had not been depleted by this date. Later, in January and February, the pecans had fallen. Because of the normal water stage in January, mast residue was probably foraged from the ground, but during the February peak, this supply was lost except for such stores as may have been on the levee or in trees. Buds of silver maple and white elm, and the few still unfallen fruits, formed a very considerable quantity of the food in February and later. It is believed that the food supply never became acute, since no unusual movements in the squirrel population were observed.

Cottontail Rabbits. — Due to protection and good food and cover, the refuge margins are very attractive to cottontail rabbits. Other upland game, especially quail, find headquarters here. At normal water level, rabbits spread out into adjacent brush, marsh, and other cover, but during each of the two floods they were forced onto the levees or certain nearby ridges. Resultant concentrations were very heavy. At one point, where the exposed levee averaged only about 10 feet in width, the senior writer, on February 17, 1942, counted 26 rabbits on one quarter-mile stretch. Cover, except for ground dens and a few brush piles, was scarce. These rabbits crouched quietly in most cases until the observer was within a few feet and then ran down the levee or leaped to one side, often into water. In such cases, numbering at least 12, they struggled to the water edge and sat quietly, although with obviously palpitating sides, until the observer passed on.

Along a wider part of the levee where brush piles were very heavy, the senior writer and a co-worker, Louis G. Brown, had occasion to walk twice daily during the period of February 15-17. No attempt to flush rabbits was made, but the average number seen at each walking of the one and one-fourth miles was 14.

The main food of these levee rabbits, at least at the time of observation, was cottonwood bark, the supply coming from the tops of hundreds of trees cut along the levee during the fall of 1941. At many places branches on or near the ground were stripped of bark, and in some cases there was unmistakable evidence of rabbits sitting on logs and large branches three feet or more above the ground in order to obtain food. The ground at most of these sites was practically covered with pellets. During a period of snow, February 11-14, beaten trails, snow-packed areas, pellet accumulations, and hundreds of urine stains, indicated the degree of use made of certain fallen tops. It is possible that this food supply attracted some rabbits to the levee prior to flooding. There was considerable evidence of rabbits feeding on sumac, elderberry, small white elm, and other woody species, as well as on bluegrass and other herbage. A few rabbit kills studied showed that the animals, even in February, were in fair flesh. Predation, considered rather light in view of the condensed population, appeared to be due mainly to minks and dogs.

Woodchucks.—A moderate to heavy woodchuck population inhabited the

levee even before flooding. During the study, 17 dead woodchucks were found, the first on November 10, about two weeks after the first crest. Some of these animals obviously had been dead for several days. The cause of death was not determined with absolute certainty, but careful field examination did not suggest disease and precluded predation in all except two or three cases. In these instances, dogs were almost certainly responsible.

Circumstances indicate that woodchucks were driven from their dens in numbers by the rising water and that, unable to find suitable unused dens or to dig others, they died primarily from exposure. All animals examined were in fair to good condition, indicating that starvation was not advanced. Several dead woodchucks were found under brush piles and possibly represent efforts to find cover. Most of the fresh digging was probably by wandering individuals. Due to the great quantities of brush on parts of the levee, which was not moved, it seems certain that only a fraction of the dead animals were found. Several woodchuck bodies had been partly, and in three cases almost wholly, eaten by raccoons, opossums, and perhaps other carnivores. It is probable, also, that dogs wholly consumed others.

Three live woodchucks were observed on snow on February 11 and 12. Two were seen at a distance of 30-40 yards. The third was this far distant when first observed by the senior writer; it was traveling toward him along the side of the levee. This animal came to a point perhaps 20 feet downhill, where it hesitated and then climbed up the slope to a distance of five feet from the writer. It hesitated again, and at a slight movement of the writer's foot it ambled off in the direction from which it had come. This woodchuck gave the impression of being lost and more or less dazed, but it was able to travel well. It disappeared under a mass of tree tops. A fourth live woodchuck was seen on February 18 at the entrance of a den.

The percentage of woodchuck-used dens in loose sand and sapling-bordered clay levee was higher than for any other species, but raccoon use was highest on the levee running through heavy timber. This fact, plus the high percentage of new dens in the other two types, dug mainly by woodchucks, suggests that this species was evicted to a greater degree from the area by high water and interspecific pressure than any other ground-denning mammal.

Raccoons.—Since shortly after the establishment of the refuge in 1936, raccoon numbers thereon have been high. This condition has been especially noticeable during the last two or three years. Since 1938 the Illinois Natural History Survey has conducted an extensive duck-banding program on the refuge, in which 15,000 or more ducks have been handled. Raccoons were attracted to the duck traps in such numbers that live trapping and release became imperative. Thirteen raccoons were so taken during the fall of 1941. Wood duck boxes have likewise been freely used by the animals, especially those on the more heavily wooded parts of the refuge. Other indications of population density were large numbers of scats on logs, in the crotches of

TABLE 3.—Density of used ground dens by species and soil-cover types on Chautauqua National Wildlife Refuge levee, Havana, Illinois, fall and winter, 1941-42.

Soil	Adjacent Cover	No. of Used Dens	No. of dens used by						Per Cent of Den: Type by Species*						Per Cent of Dens: Species by Types*						
			Woodchuck	Raccoon	Opossum	Mink	Muskrat	Rabbit	Woodchuck	Raccoon	Opossum	Mink	Muskrat	Rabbit	Woodchuck	Raccoon	Opossum	Mink	Muskrat	Rabbit	Totals
Loose sand	Weeds; willows and cottonwoods up to 10" diameter along levee	10	6	1	1	0	2	0	26	4	7	0	40	0	60	10	10	0	20	0	100
Clay	Willows and cottonwoods up to 18" diameter along levee	32	11	6	6	1	2	6	48	24	40	50	40	67	34	19	19	3	6	19	100
Clay	Heavy mature hardwood stand of 120 acres on refuge side of levee	37	6	18	8	1	1	3	26	72	53	50	20	33	16	50	22	2	2	8	100
Totals and percentages		79	23	25	15	2	5	9	100	100	100	100	100	100							

* Percentage calculations to nearest whole number.

willows, on muskrat houses, and other vantage points. Frank Bellrose, Jr., and Louis G. Brown, in February, 1941, collected in one day over 200 raccoon scats in the 120-acre timber stand bordering the levee.

Raccoons are attracted to the refuge and have increased in numbers there for three main reasons. These are complete protection, an abundant fall and winter food supply, and the general excellence of the water-marsh-timber-habitat. It is significant, however, that nearby areas, probably more attractive because of more timber, show at all seasons lower raccoon numbers. Protection and abundant fall and winter food mainly account for the greater density of the refuge population.

During the period of observation, raccoons were both active and in hibernation. In November the number of tracks on almost every part of the levee defied tracking single individuals; packed trails led to dens, both in the ground and in trees. It is believed that flooding did not drive all raccoons out of the heavy timber; indeed, there is ample evidence that during the October flood they denned in the flooded woods, in both tree cavities and in muskrat houses built at flood stage. Travel to and from such dens required that the animals swim or walk the maze of logs and debris on the water surface. Trappers reported numerous instances of raccoons taking refuge in muskrat houses. Dr. Carl O. Mohr and the senior writer found, on January 2, 1942, one animal in an old muskrat house on the Chautauqua Refuge, and obtained evidence of considerable use in this respect.

During a three-week period of low temperatures in January, 1942, the writers and others failed to find, in snow, tracks or other fresh raccoon signs anywhere on the refuge. By mid-February, however, they were active again, and packed trails were quickly re-established. Raccoon activities were carefully observed during February 10-14, when snow covered the ground. At this time, it was clear that the main concentration was on the levee bordered by heavy timber, but appreciable numbers found retreats under brush piles and in ground dens along other timber-bordered sections of the west levee. During the February flood, snow on ice did not disclose many trails leading out into the timber stand. This fact, as well as failure to find any raccoons in several scores of wood duck boxes, suggests that the animals found hibernation quarters in ground dens and perhaps old muskrat houses. Extensive live trapping in February resulted in the capture of only four individuals, a circumstance attributable in part to the abundance of natural food. The animals taken were in excellent condition. Excavation of two shallow dens disclosed one raccoon in each, neither being more than two feet below the surface. In these dens there was no litter material, the animals having bedded directly on the moist dirt floor.

It will be noticed (Table 3) that one-half of the used dens in the forest-bordered levee were inhabited by raccoons, while only 10 per cent of the used dens in loose sand, and 19 per cent in small timber-bordered clay, sheltered these animals. The attractiveness of the forest-bordered levee is undoubtedly due mainly to its proximity to the heavy timber stand.

The food of refuge raccoons throughout the fall and winter consisted mainly of ducks. It is believed that practically all birds so utilized were crippled, unretrieved kills, and birds dying late in the fall and during the winter from lead poisoning and other causes. The fall and winter food habits of refuge raccoons are discussed further under a later heading.

Minks.—The two mink dens found and listed in Tables 2 and 3 are no indication of the actual population. On the basis of track and scat abundance, and sight records, there must have been an appreciable number of minks on the refuge. It is probable that the small size of entrances to mink dens, the great quantities of brush on the most attractive parts of the levee, and possibly underwater openings, precluded the discovery of most of these dens. Also, minks in this locality frequently den in hollow willows, which are numerous on many parts of the refuge.

At daybreak on February 12 the senior writer saw two foraging minks on the forest-bordered levee. Snow covered the ground. One of the minks was on the levee proper and appeared to be trailing rabbits; the other was on a jam of floating logs and debris lodged against the levee. At the slow approach of the writer, the former ran down the levee and disappeared under a brush pile; the latter entered the water and swam toward the levee where it was lost to sight. A third mink was seen shortly after daybreak on February 14 in a willow thicket on the opposite side of the refuge. Snow tracking indicated that minks were active nightly and that they foraged over every part of the levee. On ice they traveled at least as far as the inmost fringe of willows, button-bushes, and aquatic vegetation.

Food was unquestionably abundant, consisting mainly of crippled ducks and rabbits and muskrats. Further details on food habits are given under a later heading.

Opossums.—From the data at hand, it appears that in many ways opossums reacted similarly to raccoons to flooding. Certainly, the main concentrations of the animals, as indicated in Table 2 and 3, were along the forest-bordered sections of the levee. It seems probable that flooding drove a larger percentage of opossums out of timber stands than in the case of raccoons, because of the more terrestrial nature of this species. No evidence was found of opossums denning in abandoned muskrat houses, wood duck boxes, or other cavities over water, but there are numerous records of opossums using duck boxes placed on unflooded sites.

That the opossum population was dense is certain. During raccoon trapping operations for removal under permit, five opossums were taken on the night of February 14, 1942, in seven traps on the forest-bordered levee. Numerous other individuals were caught. They were so abundant and easily captured that success in trapping raccoons was severely hindered. On release, and usually after more or less characteristic feigning, they ran clumsily off and disappeared in the first ground den or brush pile reached. It is certain that some entered dens occupied by other species.

Opossums were more active during severe cold than raccoons, although low temperatures noticeably reduced movement. Tracks were seen in January on snow when raccoons were in hibernation. One large male opossum was taken in a live trap during this period. Due to the abundance of crippled and dead ducks and dead woodchucks, there was no shortage of food. All of the score or more of opossums handled were in excellent condition.

Muskrats.—There was abundant evidence that muskrats were very adversely affected by the two floods under discussion, as reported by Bellrose and Low (1943). For this reason only a few general observations will be given here.

Both the October and February floods resulted in five-foot rises in the water level. Practically all houses and bank dens were covered and hundreds of muskrats were forced to take refuge along the levee, in willows, and on logs and other floating objects. Thus exposed, they were particularly vulnerable to predation and other forms of decimation, and there was good evidence that heavy mortality occurred. During the October flood, particularly, many houses were constructed in willows and on the tops of brush piles, logs, and stumps. Some such houses were five feet high and six feet in diameter, but most were smaller. Many new burrows were tunneled into the levee, especially in loose sand where brush piles and other cover was lacking. No special effort was made to count these new burrows, and for this reason muskrat dens listed in Table 2 and 3 have little meaning. Only those dens with entrances clearly above water level were recorded. These were probably emergency retreats.

During the fall inundation, muskrats built numerous houses in the 120-acre timber stand, which is of the mature floodplain type. These houses were most common near the edge of the woods bordering the willow and buttonbush flat, but a number of houses were 100 yards or more back in the timber stand. Construction materials consisted of sticks and leaves, there being almost no herbaceous vegetation at hand. Such houses were often on logs, in the crotches of twin trees, and on tree tops. Due to the three- or four-foot depth of water here, none rested directly on the ground. Numerous instances were found where hollow trees were inhabited, all or nearly all openings to the central cavity being tightly plugged with leaves. Cases were found where house-like structures were placed over the open end of hollow logs and stumps, the animals using the cavity as a retreat. These stick-and-leaf houses were well built, and it taxed the strength of a man to tear them apart. Practically all houses so treated for study purposes contained a definite cavity with one or more entrances from the lower side. These dens were 12 or 14 inches in their longest dimension.

Muskrat behavior along the levee at flood peak was characteristic. They sat quietly throughout the day on the low banks, on logs or trash, or in willows. At times, particularly in October, they were not sufficiently disturbed by passersby to dive into the water. It may be that they were too confused

to react normally. During the receding stages of the floods they usually did dive when approached, indicating some conditioning to the emergency. In February, scores were observed on the nearby submerged levee along the west side of the refuge and at other points. Most of these muskrats were sufficiently rational to dive at our approach. At the time of the fall flood they were less experienced, the population at this time containing a high percentage of kits. This combination of factors, it is believed, explains the difference in reaction during the two flood periods. Predation and total mortality were certainly greater during the fall flood.

The food of muskrats during these flood periods consisted in part of cottonwood and willow bark and white sweetclover roots. The few carcasses examined were in fair condition.

Red Foxes.—Only two red foxes were seen on the levee, both on February 13, 1942. One trotted past the senior writer, and the other was jumped by him in weed cover on a south-facing slope. A number of other sight records have been reported, and tracks were common. On January 2, in light snow on ice, Dr. Mohr and the senior writer found several trails and at least two kills, these being a rabbit and a mallard duck. These signs were along the southeast shore of Lake Chautauqua in heavy willow-buttonbush cover. The dens of these animals were undoubtedly in the refuge levee.

Skunks.—Several skunk trails were followed, especially in February, but no dens were found. There was some evidence of feeding on dead woodchucks and ducks. Three skunks were seen by car light in November, 1941, in a field near the refuge. Ample food and excellent denning sites qualify the outer refuge margin and the levee as a good skunk habitat.

Feral Dogs. — Dogs range the levee at will and are almost certainly attracted by abundant food during the fall and winter. Dead ducks were probably the main item, but dogs evidently fed at times on dead woodchucks. There was considerable evidence of den destruction by digging.

Moles, Shrews, and Mice. — Only incidental notes relative to moles, shrews, and mice were recorded. Included were 20 newly made tunnels of the common mole (*Scalopus aquaticus*), all on top of the levee. These were observed in November and early December, while the soil was still unfrozen. The effect of flooding on moles inhabiting the 120-acre riverbottom forest and other low wooded areas, probably the best mole habitat on the refuge, is not known in detail. Two short-tailed shrews (*Blarina brevicauda*) were found under decayed logs on the levee, and the junior writer found a dead woodchuck, the tongue of which was believed to have been eaten by shrews. Meadow voles (*Microtus ochrogaster*) were fairly common along parts of the sand levee. Trails typical of those made by these voles were noted in German millet, which had been planted on the levee as a soil stabilizing agent. They also occurred in other vegetation. It seems likely that white-footed mice (*Peromyscus*) were attracted by the millet and other grass and weed seeds, since several nests were in vines and brush nearby. No live white-

footed mice were seen. Likewise, no flying squirrels were seen, but they are known to occur on the refuge. Two other occurring species, the striped ground squirrel (*Citellus tridecemlineatus*) and the eastern chipmunk (*Tamias striatus*) were in hibernation at the time of the study.

Effects of Waterfowl Concentration

The Chautauqua National Wildlife Refuge is the most important fall concentration area for waterfowl in Illinois and one of the most important on the Mississippi flyway. At the peak of the fall migration, up to 700,000 ducks may be present on the area, and some 30,000 to 50,000 reside here throughout the winter. About 90 per cent of these ducks are mallards, but practically every other American species, in addition to geese, scoters, and other waterfowl, are represented.

Waterfowl Available to Carnivores

Legal hunting outside the refuge, particularly off the Quiver Lake and Clear Lake levees, is heavy. Long-range shooting is common, and crippling losses are more or less excessive. Kills falling on or near the levee are retrieved with difficulty, and more important from the standpoint of flesh-eating mammals is the comparatively large number of ducks fatally hit, but which fall well inside of the refuge and later drift in to shore. These ducks, in addition to mortality from cripples, lead poisoning, and other causes during winter, far exceed the needs of predatory animals resident on and attracted to the refuge. An estimate of the waterfowl available to carnivores along representative parts of the levee is given in Table 4.

From Table 4 it is clear that several times more birds were available near hunting grounds than away from them, but it is also evident that dead and crippled ducks were scattered widely around the refuge. Mallards and lesser scaups were the most important species. Mallards showed the highest percentage of cripples, possibly indicating a greater hardiness in this species. It should be remembered that the above data are conservative because they include only the dead and crippled birds seen. The actual number includes also those birds eaten previous to inspection and those present but not found at that time. From the number of dead cormorants found it appears that hunters lose few opportunities to shoot them.

Effect of Waterfowl on Food Habits of Predators

That flesh-eating birds and mammals should take advantage of the food supply represented by dead and crippled ducks is to be expected. In any concentration of birds such as occurs annually on the Chautauqua refuge natural mortality alone must result in considerable food for carnivorous forms, and of itself would undoubtedly attract them to the refuge. The influence of natural mortality and the opportunity for predation on flesh-eating levee populations is not known, but the evidence strongly suggests minor import-

TABLE 4.—Dead and crippled waterfowl on Chautauqua Refuge, fall, 1941.

Date 1941	Section of Levee	Length, Miles	Mallard		Black Duck		Pintail		Lesser Scaup		Blue-wing Teal		Gad-wall		Ruddy Duck		Buffle-head		Cormo-rant		Miscel-laneous[1]	
			Dead	Crippled	Dead	Crippled	Dead	Crippled	Dead	Crippled	Dead	Crippled	Dead	Crippled	Dead	Crippled	Dead	Crippled	Dead	Crippled	Dead	Crippled
Adjacent to Shooting Grounds:																						
11-11	Clear Lake	.75	6	10	0	2	0	0	4	1	1	0	0	1	1	0	0	0	5	0	0	0
11-12	Quiver Lake	.75	4	7	0	1	0	0	4	0	0	0	0	0	1	0	0	0	5	0	0	0
11-21	Quiver Lake	.75	2	0	0	0	1	0	17	5	0	0	0	0	3	0	0	1	1	0	0	0
11-25	Quiver Lake	.75	2	0	1	0	0	0	25	4	0	0	0	0	0	0	0	0	0	0	2	0
One-half Mile or More from Shooting Grounds:																						
11-11	Southeast Bluff	1.00	2	3	0	1	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0
11-13	Quiver Creek	.50	2	3	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
11-24	Quiver Creek	.50	1	1	0	0	1	0	1	4	0	0	0	0	0	0	0	0	0	0	1	0
11-25	Northwest	.75	1	4	0	1	0	0	1	2	0	0	0	0	0	0	0	0	1	0	0	0
11-25	Illinois River	2.00	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0
11-26	South Bluff	1.25	1	1	0	0	1	0	1	4	0	0	0	0	0	0	0	0	0	0	0	0

1 Grebes, Coots, etc.

ance when compared to the food made available by hunting. Of the several scores of ducks handled on the levee by the writers, all had been killed or crippled by shooting. This small sample, while not conclusive, certainly emphasized the importance of hunting on food availability in the case under discussion. It is recognized that ducks dying or becoming disabled through natural causes are likely to be widely scattered and hence not apparent or easily subjected to evaluation.

The prehunting season foods of refuge predators were not studied formally, but extensive examination of both raccoon and mink scats in the field failed to disclose duck feathers in any appreciable quantity during the summer and early fall. The main foods of raccoons at this season were corn, wild grapes, pokeweed berries, persimmons, crayfish, fish, and insects. Minks, at this season, fed mainly on crayfish, fish, and muskrats.

It is clear, however, that concurrently with the availability of dead and crippled ducks the food habits of flesh eaters shifted abruptly, and that ducks became the principal food item. The degree to which raccoons used waterfowls is shown in Table 5.

TABLE 5.—Post-hunting season foods of raccoons on Lake Chautauqua National Wildlife Refuge, fall and winter, 1941-42, based on 140 scats.

Food	Occurrence		Bulk	
	Number	Per cent	Volume in c.c.	Per cent
Waterfowl, almost entirely ducks	78	55.7	3,629	51.8
Persimmon, *Diospyros virginiana*	28	20.0	1,307	18.7
Corn, *Zea mays*	28	20.0	811	11.6
Wild grapes, *Vitis* spp.	8	5.7	301	4.3
Fish, mainly carp and gizzard shad	8	5.7	157	2.2
Insects, mainly water beetles	12	8.5	140	2.0
Crayfish	6	4.2	114	1.6
Pokeweed, *Phytolacca americana*	4	2.9	99	1.4
Woodchuck, *Mormota monax*	4	2.9	95	1.4
Cottontail Rabbit, *Sylvilagus floridanus*	4	2.9	90	1.3
Nightshade, *Solanum* spp.	8	5.7	40	.6
Miscellaneous: Apples, other fruits, earthworms?, etc.	16	11.4	217	3.1
Total and percentage			7,000	100.0

The data presented in Table 5 are not the result of detailed laboratory examination of scat material. The procedure used here is somewhat similar to the field method of analyzing game bird foods described by Davison (1940). It is simpler, more rapid, and probably less exact than the technique employed by Davison and his colleagues. The process here to be described does not indicate traces, and the volume of miscellaneous food is high. How-

ever, the writers feel that it does indicate trends accurately and that its use is justified when time and facilities are limited and when only a general local picture is required. It is not recommended for precise food habits work.

The procedure is simple. Any given scat to be examined is merely broken up and the various important items separated. Flat surfaces, such as flat-topped stumps, large smooth logs, bridge floors or sills, or newspaper, facilitate this step. Ocular estimates of the volume of separate items in per cent are then recorded. Surprising accuracy in this respect can be developed, but it should always be kept in mind that the absence of mechanical measurements leave such estimates constantly open to serious error. It would be but little more time consuming to measure the materials roughly in the field. Both measurements and ocular estimate under field conditions are subject to the error accruing from differential moisture content. Entries for typical scats read as follows:

"No. 1: 80% duck feathers, 20% miscellaneous";

"No. 23: 100 % duck feathers";

"No. 60: 25% grape, 50% persimmon, 15% pokeberry, 5% *Solanum* seed, 5% miscellaneous.."

The summation of all percentage values, by items, and these quantities divided by 100, gave the number of scats composed of each food. Volume was calculated simply by multiplying the number of scats in each case by 50 cc., approximately the average bulk of 419 Illinois raccoon scats as determined by Yeager and Rennels (1943). Percentage values may then be readily calculated from these quantitative data.

That the method described here is rapid is emphasized by the fact that the information presented in Table 5, resulting from field examination of 140 scats, was gathered in less than three man-days. In this case, the material for examination was abundant and readily accessible.

Despite the abundance of waterfowl, and the fact that this item represented about one-half of the total food after the opening of the hunting season, wild fruits still formed an appreciable part of the diet of refuge raccoons. That fruits should rank so high is due in part to their abundance and availability. Persimmons, grapes, and pokeweeds grow in quantity on or adjacent to the levee, and further supplies are to be had just off the refuge. A number of fields, usually planted to corn, join the refuge boundary.

In collecting scats for this study, care was exercised to reject obviously old material, but even so, some scats containing corn, persimmons, and other fruits may have been of pre-hunting season origin. If this is the case, the figures depicting the importance of ducks as post-hunting season foods are conservative. The writers have no doubt as to the date of origin of feather-containing scats, this confidence being borne of repeated pre-season examination of scats, in which duck feathers appeared only in negligible quantity.

In 26 mink scats collected in November and December, mainly along the forest-bordered levee, feathers, almost entirely of ducks, made up the entire

content of 18, and were represented in 23. Fish, rabbits, and muskrats were the other iems occurring in appreciable quantity. The few opossum scats examined contained feathers, woodchuck hair and a miscellany of seeds. No data were obtained relative to the foods of red foxes and skunks.

Field observations other than examination of fecal material amply indicated the utilization of dead and crippled ducks by flesh-eating animals. Raccoons usually fed on birds where they were found. Tracks in the sand or snow revealed this detail. On November 12 the writers found nine partly-eaten ducks along a half-mile of the Quiver Lake levee; and on November 25, a total of 19 partly-eaten ducks was found on the same area. It appeared that opossums also consumed the birds where found, but minks usually dragged them to cover, mainly under logs or brushpiles.

The number of crippled and dead ducks present on the above dates is given in Table 4. The turnover in ducks available to carnivores on the levee proper was roughly at weekly intervals. The quantity varied with the degree of shooting, which is largely governed by weather conditions. This source of food lasted for some time after the hunting season closed, in Illinois, on December 16, and mortality from lead poisoning and other causes added to the supply after this date. Remains of recently eaten ducks were observed as late as mid-February. Numerous ducks fell dead or died in water and later became entangled in the rafts of logs and other debris along both sides of the levee. Cold water prevented decay, and in many instances feathers and other remains showed that these birds were pulled out of the water and eaten. Others, frozen in ice, were eaten as far below the ice surface as accessible. Some of these, lodged in vegetation, were considerable distances from the shore.

Gulls and bald eagles were also attracted to the dead and crippled ducks and are known to have fed thereon. Gulls, chiefly herring and ring-bill, utilized to a marked degree dead ducks, cormorants, and other birds frozen in the ice.

It is considered that the dead and crippled birds consumed by predators, especially by fur animals, represents desirable utilization. It results, in part, in the production of a valuable fur crop, the harvesting of which is simplified by the concentrating effect of an abundant food supply during the trapping season. Moreover, this ready availability of food to predator populations probably results in less destruction by them to healthy waterfowl.

Summary

1. The Lake Chautauqua National Wildlife Refuge is a bottomland area of about 5,000 acres in Mason County, Illinois. It was established in 1936 and is now one of the most important duck concentration areas on the Mississippi flyway.

2. About 85 per cent, or 4,250 acres, of the total area is water, the level of which is maintained by dikes. The levee is of three main soil-cover types: loose sand, with weed and small willow cover; sandy clay, with weed, vine,

and sapling-small tree cover; and sandy clay, with weed, vine, and heavy tree cover. Only the latter type was bordered by a mature forest stand. The sand levee is only about three years old, while most of the other is 10 to 20 years old. This embankment affords the best site for ground dens anywhere on the north, south, and west sides of the refuge.

3. Studies on levee ecology, and the effects of flooding and waterfowl concentration on mammals, are reported. Flooding occurred both in the fall and winter, further concentrating certain mammal populations. Legal hunting near the refuge made available to carnivorous speecies an abundance of unretrieved and crippled ducks.

4. The effect of flooding on mammals ranged from heavy mortality in the case of woodchucks to apparently little basic change in the behavior of minks. During the October flood much new den construction, mainly by flooded-out woodchucks, was evident. Seventeen dead woodchucks, presumably dying from exposure, were found. Competition for ground dens was severe. In the absence of tree cavities, raccoons and opossums freely used ground retreats. Seventy-nine of the total of 114 ground dens were obviously in active use; others probably contained hibernating or inactive animals, or may have been flooded. Dens were seven times more abundant on the sappling bordered levee, and 17 times more abundant on the mature forest-bordered levee, than on the newly constructed levee of loose sand. Seventy-two per cent of the raccoon dens and 53 per cent of the opossum dens were in the forest-bordered levee.

5. Hundreds of dead and crippled ducks were available to refuge carnivores. There were several times more ducks on the two sections of the refuge near legal hunting grounds than on sections away from them, but dead and crippled birds were widely scattered over the entire refuge. Mallards and lesser scaups were represented in largest numbers.

6. Carnivores took immediate advantage of the sudden availability of a new food supply. In 140 post-hunting season scats of raccoons, feathers, mainly of ducks, occurred in 55.7 per cent, and made up 51.7 per cent of the bulk. In 26 mink scats of post-hunting origin, duck feathers were present in 23, and constituted the entire content of 18. Despite the abundance of ducks, wild fruits and field corn composed nearly 40 per cent of the late fall and winter foods of raccoons. Dead and crippled ducks taken by carnivores would otherwise have served no useful purpose.

REFERENCES

BELLROSE, FRANK C., JR., AND JESSOP B. LOW. 1943—The influence of flood and low water levels on the survival of muskrats. Jour. Mammal. **24**(2):173-188, illus.

DAVISON, VERNE E. 1940—A field method of analyzing game bird foods. Jour. Wildlife Mgt. **4**(2):105-116.

YEAGER, LEE E. AND R. G. RENNELS. 1943—The raccoon in an Illinois river bottom area: fur yield and fall foods. Jour. Wildlife Mgt. **7**(1):45-60, illus.

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Paratyphoid Infection in the Northern White-footed Mouse in Central Iowa

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On August 3, 1940, trapping of the white-footed mouse, *Peromyscus leucopus noveboracensis* (Fischer), was begun both in the Des Moines River Valley in Boone County and in the woods surrounding Iowa State College in Story County. These mice were to be used as experimental hosts for rodent warble infection. From the date trapping commenced until November 2, 1940, several mice were found in the live traps either dead or wavering on their feet. Others died after being in captivity from two to five days. This condition led to the following investigation.

During the period from August 3 until September 13, 240 mice were trapped in the above mentioned areas. All of them succumbed because of causes unknown to the author at that time. On September 3, several of the dead mice were autopsied in the Veterinary Pathology Laboratory of Iowa State College and biochemical tests were made of cultures grown from their livers. The isolated organisms were found to be *Salmonella typhimurium* (Loeffler) Castellani and Chalmers, the mouse typhoid bacterium belonging to the paratyphoid group.

All traps were then brought in from the field and they were sterilized along with the cages used to house the mice. Every possible precaution was taken to avoid contamination. On September 15 sterilized traps were then set out in the same localities previously trapped and the cages were removed to new quarters. The traps were sterilized before each resetting and the cages were sterilized after each change of occupant. All mice were then isolated when brought into the laboratory and precautions were taken not to spread any existing infection from cage to cage by contact.

Of the seventy mice caught from September 15 through November 2, last date on which *Salmonella* was detected, nineteen (27%) were found to be infected with *Salmonella typhimurium*. Fifteen of these had been killed immediately upon removal from the traps, whether or not they seemed healthy, to

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ascertain whether the bacterial infection was rampant in nature or whether infection was spread only after the animals had been caged. Several mice found wavering on their feet in the traps were not taken in; others that died soon after capture were not autopsied since it was thought that the weakness might have been caused by heavy parasitism with the rodent warbles. Had all these animals also been examined, the amount of infection might have been found to be even greater.

Infection was found to be greatest during the warmer part of the period during which the animals were trapped. It was very high during September, lower in October, and it disappeared completely after November 2. Although nothing certain is known about the cause of death of the caged mice during August, it is probable that most of them died from paratyphoid infection acquired in the wild or spread in the laboratory. Since trapping was not carried on during the winter, except on a few occasions, it is not known if there was any infection prevalent during that part of the year. The last date of regular trapping was November 30, 1940.

Salmonella typhimurium was isolated by Loeffler in 1892 from a natural outbreak in mice. Serological and biochemical reactions show the following to be synonymous with it: *Bacillus pestis-caviae* (Wherry), *Bacillus psittacosis* (Nocard), *Bacillus aertrycke* (deNobele), and *Salmonella aertrycke* (Castellani and Chalmers) (Bergey, 1939).

Salmonella typhimurium is widely distributed geographically, occurring in numerous species of mammals and birds. It produces an intestinal infection which is often fatal in rats, mice, guinea pigs, sheep, calves, horses, chickens, turkeys, parrots, and pigeons. All recorded cases of mouse paratyphoid are concerned with animals in laboratory cultures. As far as the author has been able to discover, the case described in this paper is the first to show the existence of paratyphoid infections in wild mice. Characteristic symptoms of mice infected with this organism are increased temperature, general weakness, abnormal closing of the eyelids, and diarrhea. The animal finally becomes too weak to support itself, topples over, and succumbs.

Epidemics of food poisoning in man have long been attributed to this organism (Jordan, 1925) but it has recently been shown that *Salmonella schottmuelleri* (Winslow *et al.*), a very closely allied species, is the true causative agent (Merchant, 1940).

It is almost impossible to predict the status of *Salmonella* infection in nature, since the dead animals are seldom found in the wild. In tests made during a rat eradication program on the Pacific Coast, Dr. N. E. Wayson found that out of 775 rats examined, 3.9 percent were carriers of *Salmonella typhimurium* (Meyer and Matsumura, 1927). From studies made with laboratory strains of albino mice, it has been found that certain strains are naturally more resistant than others and that immunity can be acquired (Hetzer, 1937 and Schott, 1932). To what extent this is true in nature is unknown.

REFERENCES

BERGEY, D. H. ET AL. 1939—Manual of determinative bacteriology. 5th edition. The Williams and Wilkins Co., Baltimore.

HETZER, H. O. 1937—The genetic basis for resistance and susceptibility to *Salmonella aertrycke* in mice. Genetics **22**:264-283.

JORDAN, E. O. 1925—The differentiation of the paratyphoid-enteritidis group. Jour. Infec. Dis. **36**:315.

MERCHANT, I. A. 1940—Veterinary bacteriology. The Collegiate Press, Iowa State College, Ames, Iowa.

MEYER, K. F. AND K. MATSUMURA. 1927—Incidence of carriers of *B. aertrycke (=B. pestis-caviae)* and *B. enteriditis* in wild rats of San Francisco. Jour. Infec. Dis. **41**:395-404.

SCHOTT, R. G. 1932—The inheritance of resistance to *Salmonella aertrycke* in various strains of mice. Genetics **17**:203-229.

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Ecological Composition of Pulpwood Forests in Northwestern Maine

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Introduction

Within the State of Maine are few, if any, relicts of the original northeastern coniferous forest. Extensive areas of forest land are covered with second-growth forest, the main source of pulpwood for the local papermills. Silvicultural considerations have had little weight in determining the management of these forests in the past. Demand for and accessibility of timber have regulated the extent of each year's cut. Modern methods of operation, particularly clear-cutting, suggest the future value and usefulness of silvical and ecological information pertinent to the nature of these second-growth forest communities. Sound silvicultural practices can be initiated and applied successfully only as ecological and silvical information accumulates.

The Swain and Reed Lumber Company of Roxbury, Maine, provided special facilities in the summer of 1940 which made possible an ecological survey of the pulpwood forests in the general vicinity of the watershed of Swift River, a tributary of the Androscoggin River, located in northern Oxford County, Maine. After reconnaissance, several stands were selected as representative of the pulpwood forests of the region, and these were studied intensively on a phytosociological basis. This is a report on the findings of the study with conclusions drawn from the data obtained.

Historical

The physiognomy of the present-day pulpwood forests in northwestern Maine is clearly separable into two major aspects; the mixed spruce-hardwood forests, principally composed of yellow birch, red spruce, sugar maple, balsam fir, beech, and white birch; and the nearly pure coniferous stands of red spruce and balsam fir. These forests, covering vast acreages, are, of course, second-growth resulting from a series of operations which have extended well over a century. From about 1800-1870 the land was cleared for agriculture. Only the choice white pine was commercially valuable and aside from its localized selective cutting, the forests were removed by girdling and burning the trees. Then saw mills were built near the mouths of the rivers, thus establishing a demand for the best quality spruce which was selected from the more accessible forest areas bordering streams. This selective cutting of spruce for saw timber continued for about 20 years, and gradually the best spruce was removed even from the headwaters of the larger streams and their main tributaries.

This period was terminated when pulpwood came into use. In the Swift River Valley, the first wood was used for pulp about 1880. Spruce exclusively

was demanded in this initial phase of pulpwood operations. The natural transition in logging practice was to a heavy spruce cut instead of the former selective method, followed by diversion of the best quality spruce to the saw mills, and the remainder to the paper mills. Poplar was tried for pulpwood before 1890 but did not come into general use until later. With the decline of available spruce in the 1890's balsam fir was cut for pulp, and many of the forested areas were re-operated for the balsam fir and the small spruce left from previous cuttings.

The widespread use of spruce and fir as the most desirable species for pulpwood continued locally until about 1912, when a small percentage of hardwood was first used successfully. Although spruce and fir are still considered most desirable as pulpwood, the proportion of hardwood used in the paper mills which serve the Swift River region has been increased steadily until today 100 percent hardwood can be used successfully for some purposes. The increased importance of hardwood permitted the re-working of most forest lands. Today it is a common practice to cut everything of merchantable size within a stand, since both softwoods and hardwoods find a regular market at the paper mills.

The practice of clear cutting has only recently become general in northwestern Maine. Its effects upon reproduction and subsequent forest composition are still uncertain. The application of silvical principles and practices has not yet been well established. This is partly because clear cutting of both hard and softwood species is new and silvical information concerning its effects is lacking. It is also because experience has decreed it necessary to gauge the season's cut of pulpwood in any single operation solely in proportion to the demand, which has always been irregular and rather unpredictable. Economic considerations and immediate accessibility at the time a tract was operated for pulpwood have often resulted in the removal of stands, the majority of whose trees exceeded the minimum size class acceptable to the mills, but which were not at the stage of maximum yield per acre.

The revolutionary changes in transportation of the past 60-70 years have contributed strongly to the methods and nature of lumbering activities in northwestern Maine. Until about 50 years ago all lumber was driven from its source to the mills along the myriad water-courses of the region. This practice gave the lumber industry decidedly seasonal characteristics; fall and winter were spent in cutting; winter in skidding the timber to water; spring and early summer in driving the logs to the mills, as a rule. Furthermore, this method of transportation necessarily restricted operations to areas near enough to the water for convenient handling. During the 1890's came a period when railroad hauling predominated. Temporary lines, built into previously inaccessible areas, made available vast acreages, until then practically untouched. These operations were more expensive than transportation by water, they were on a large scale and usually they were aimed at immediate returns.

During the past fifteen years the truck has replaced the railroad in logging. In fact, all of the railroads in the Swift River area, even those of a relatively

permanent nature, have now been abandoned, for they derived their major revenue from lumbering activities.

Except for the necessity of peeling much of the pulpwood in the spring and early summer, the use of trucks on either winter or summer wood-roads has removed in large measure the seasonal nature of pulpwood operations in the region. Furthermore, these year-round operations are carried on profitably even on a small scale. Selective cutting of small stands in localized and heretofore inaccessible areas is now possible.

Another change has occurred within recent years. Lumber and pulpwood companies are increasingly regarding their forest lands as permanent investments. There is even an accelerating tendency for farm and pasture land to be abandoned until whole townships may be returned to forest, under the control of lumber companies.

With the trend to permanent ownership and a long-term investment — attitude on the part of operator-owners, coupled with new operational methods afforded by the use of trucks, it is inevitable that sound silvicultural practices will reach even the more remote pulpwood lands in northwestern Maine. In the establishing of fundamental principles upon which a sound silviculture may be based, ecological studies of the nature of pulpwood forests can contribute materially. Such studies are noticeably lacking for the state of Maine.

Literature

Purely ecological papers dealing with the pulpwood forests of Maine or even the northeast are few but several forestry publications are concerned with second-growth forests in the region. Some deal specifically with Maine, others are of wider scope. Those papers and parts of papers are chronologically reviewed here which indicate the progression of silvical and ecological ideas prevalent in the region of this study.

In a foreword to the second annual report of the Forest Commissioner of Maine (1894), Charles E. Oak summarized lumbering practices to that time. He was greatly concerned over the wastefulness of methods and predicted the necessity for state regulation of certain procedures unless they were corrected. Many of the matters of concern have corrected themselves through the years.

In this same report Austin Cary (1894) suggested numerous forestry problems which should be investigated. He indicated that growth and yield data should be compiled so that the potential values of stands could be estimated. He recommended studies of different types of selective cutting; of sizes and ages to cut; and of development of second growth on cutover lands to determine time and quality of second cuttings. Considering that vast acreages of timber were being indiscriminately exploited in Maine at the time and that no obvious concern for a future supply influenced prevalent practices, Cary expressed especially advanced ideas. It is of added interest to the ecologist that Cary discussed the relationship of pine and birch to fire and that he

recognized their successional nature. Furthermore, he postulated a universal return to the original virgin state after cutting of the forests, if they then were freed from man's activities. The recognition of succession and ultimate stability with time (climax) were exceptional ideas for 1894.

In the third report of the Forest Commissioner, Cary (1896) summarized his survey of Maine forest resources, one of the earliest studies of this sort for the state. He covered a large part of the state studying forest resources and lumbering with particular reference to spruce. The best virgin spruce was found on the upper Androscoggin River and in the Rangeley Lakes district. He called this area "the chosen home of the spruce." "No other part of Maine . . . ever had any such spruce stand." Although red spruce was cut as early as 1856 on the lower reaches of the river, much of this forest about the headwaters was still virgin in 1896 and the railroads were just beginning to push into the territory.

Cary classified the forest into (1) swamp, (2) intermediate lands with mixed stands, and (3) mountain land, the higher slopes with pure spruce. His observations caused him to condemn irregular cutting because of the resulting blowdowns. He argued strongly for clear cutting because he believed this would permit birch stands to establish themselves. Since such birch stands favor the underlying young spruce reproduction, Cary contended that, upon reaching a merchantable size in about 30 years, the birch could be cut, leaving the site to flourishing young spruce trees. Although present-day acreages of white birch do not entirely support his observations, Cary believed in 1896 that white birch would cover large areas within second-growth forests where blow-downs and fires occurred. His observation that birch reproduction predominated on old yards and sluice-ways was correct.

Another silvical problem raised by Cary was the eventual nature of these forests if spruce were continually cut. He presumed that hardwoods would be favored and spruce would decrease. His recommendation that the hardwoods be girdled was not followed. Today girdling might be more strongly urged for the cull and wolf tree hardwoods left on the clearcut areas.

Poplar had already been used successfully for pulp and this led Cary to urge the use of other hardwoods. This he contended would be the salvation of forestry on second-growth lands.

Throughout the report one is impressed by the practical and scientific approach, unusual in the period. Cary pleaded continually for *forestry* not *lumbering*. He recognized that management was not only desirable but an absolute necessity if lumber were to be produced indefinitely.

The first intensive study of Maine spruce on cut-over lands was made by Hosmer (1902). His work was done in the Moosehead Lake district (Piscataquis County) but his observations were much more widely applicable. His was the first publication of the widely used classification of forest types and their associated sites: (1) Swamp, (2) Flat, (3) Spruce-Hardwood, (4) Spruce Slope, with such satisfactory descriptions that they have been used

again and again, almost without change of wording. Observations were recorded on spruce reproduction with the suggestion that good and bad seed years are cyclic and that trees less than five inches D.B.H. produce little or no seed. It was suggested that the nature of the seed bed is of greater importance in germination and survival than slope, aspect or altitude. The moss-duff cover of the spruce slope was rated as the best seed bed, and then follow in decreasing quality, decaying wood, hardwood leaf litter, and mineral soil. It was emphasized that the greatest mortality of seedlings is between six-inch and two-foot height classes and that the number of seedlings is correlated with depth of humus. Thus, the more intensive the lumbering, the greater the disturbance of humus, and the fewer the spruce seedlings.

The effects on future stand composition of the continuous removal of spruce was already a matter of concern in 1896 (Cary). In 1907, Moore and Rogers published a survey of their observations on the response of fir and spruce to several lumbering practices. They contended that fir is less tolerant than spruce and consequently best spruce reproduction comes under dense stands while fir predominates in more open areas. They stated that fir matures at an early age, is subject to breakage in the larger size-classes and to rot after 50 years, and that beyond this age fir does not recover well after suppression. They observed that windfall of pure spruce is followed by pure fir, and that spruce-hardwoods, when blown down, are followed by fir-hardwoods. Further, these authors stated that the proportion of fir in the spruce hardwood type actually doubles after each cutting. When the spruce slope type is clear-cut a two to twenty percent increase of fir may occur. Although the balsam fir appeared to be increasing disproportionately under these several conditions, its early maturity and subsequent decline were believed to nullify its importance to some extent in the region. However, it still was considered a significant competitor which, throughout its short life, might retard growth of the associated spruce.

It is of interest that before 1907 a large lumbering company operating in the Androscoggin-Rangeley area recognized the possibilities of applying forestry principles sufficiently to hire Austin Cary as a professional forester. Cary (1907) discussed his attempts to initiate new practices. Opposition came not from the lumbermen but from the field crews who were by long habit set in their ways. Radical changes were impossible but he made some progress in reducing waste; saving down-timber; and preserving advance reproduction. These innovations were possible only through constant inspections of work and continuous pressure on woods bosses. The introduction of cutting contracts which specifically indicated the desires of the owners, he felt, was a strong influence in improving the wasteful and often destructive methods so characteristic of operations at the time.

A bulletin on balsam fir by Zon (1914) deals with features about the species ranging from life history and physical properties of the wood to recommendations for its silvicultural management. The tree does not produce seeds, usually, until 30-35 years of age but then has a crop annually with good yields coming at least every fourth year. Germination (20-30 percent) takes place

on any substrate that is moist. Light requirements are greater than for spruce and increase as the tree matures. After a slow start growth is rapid between 5 and 60 years, then declines until 80 years after which it is very slow. The close relationship of spruce and fir is recognized in the statement that both respond equally to silvicultural treatments. Zon believed that clear cutting necessitated planting to perpetuate these softwoods and recommended a system of selection cutting to assure reproduction of spruce and fir and possibly to increase the spruce.

Murphy (1917) brought together a mass of information concerning red spruce acumulated from its entire range through several years of observation. The use of spruce for lumber was still on the increase but the demand for spruce pulp was such that approximately one-half the cut was used for each. By 1917 enough abandoned agricultural land had grown up to spruce so that *Old Field Spruce* was recognized as a fifth forest type to be considered in spruce studies.

The results of experimental studies indicated that spruce produces some seed every year and that exceptional seed crops may be anticipated at intervals of 3 to 8 years. Seeds are 50-90 percent perfect and of these 60-80 percent germinate. With an exceptionally low light requirement, the important factor in seedling survival is a continuuos supply of soil moisture whether the seed bed be mineral or organic. The shallowly rooted seedlings are very susceptible to dessication in deep organic soil. This gives balsam fir an advantage in competition for it produces crops of seed every year, its seedlings grow faster and its roots penetrate much more deeply than those of spruce. Among other factors contributing to reduce reproduction is the tendency of its seeds in the forest to germinate in the fall. Most of these do not survive. Fir, on the other hand, rarely germinates in the fall.

Other sections in the paper summarized susceptibility to injury, data on increment, slash disposal, and cutting methods. Selection cutting was recommended as highly desirable but scarcely practical except perhaps under state ownership. Cutting to a diameter limit, a form of selection, was being rather widely used at this time in the spruce region. The difficulty of getting the loggers to use this method with success was emphasized.

Linn (1918) reported his observations of some methods used in lumbering operations in New Hampshire. He noted that cutting softwoods to a 12-14 inch diameter-limit in the spruce-hardwood forests tended to increase the number of hardwoods without speeding growth of those already present. If both hardwoods and softwoods were cut to this limit the reproduction of the latter was maintained but fir increased cost of logging. In pure spruce, particularly spruce flat, clear cutting gave ample softwood reproduction and a reduced cost of logging.

The method of diameter-limit cutting was adopted on a wide scale because it supposedly maintained the softwood population and at the same time prevented blowdown. McCarthy (1919) argued that neither of these ends was

accomplished by the method. In fact, he maintained that the proportion of hardwoods increased and that windfall losses remained high. He stated that, if a large percentage of softwoods is desired, cutting of hardwoods must be severe enough to destroy the deciduous crown cover. He believed that such a practice would also contribute to the production of better hardwoods since they are likewise suppressed by an old crown cover.

Moore (1920) made observations of the root form of seedlings of spruce and fir seedlings which led him to emphasize moisture rather than light as the important factor in establishment. As suggested by others, he found spruce seedlings rooted only in humus while fir had at least one small root extending into mineral soil. This gives fir a slight advantage under conditions which desiccate the humus. At maturity both spruce and fir were found to possess mostly lateral roots, the former having a somewhat more finely divided network of fine fibrous roots. Beech and hard maple have their major roots in the same superficial soil strata as the softwoods. Later, Moore (1926) studied seedling development under experimental conditions. Both spruce and fir germinated better on mineral soil than on humus and in shade than in sunlight but, under the same experimental conditions, growth was always better in the open than in the shade.

Although girdling was recommended as a silvicultural means of controlling proportions of hardwoods as early as 1896 (Cary) nothing came of it. Churchill (1927) described the method in detail including costs and results of perhaps the first experimental girdling work done in the region by a commercial concern. Accurate records indicated that, even with the higher costs involved in the small operation, the company would be amply repaid in greater returns from the treated stands. In 1928 Cary summarized his arguments and those of others for girdling hardwoods. He gave approximate costs and showed that the method can be made to pay in terms of increased softwood growth.

Westveld (1930, 1931) discussed certain silvicultural aspects of the management of spruce stands and the nature of the reproduction on cut-over pulpwood lands in the Northeast. His was the first emphasis of the importance of advance reproduction in the establishment of the forests which follow pulpwood operations. His findings indicate that, normally, reproduction is abundant on cut-over lands almost immediately after cutting. This advance reproduction was already present beneath the old stand and was released by the cutting. If this advance reproduction is adequate in sizes from 2-5 feet tall, the new stand is established much more rapidly than when the 5-6 inch trees are depended upon for seed source, since the latter produce sufficient seed only after a long period of time. His data show conclusively that spruce and fir seedlings are most abundant directly after cutting, but decline thereafter. Without the advance softwood reproduction at the time of cutting, hardwood seedlings and sprouts gain a strong advantage before the immature softwood trees left from the previous operation have ever produced an abundant seed supply.

Although Westveld suggested that soil type may be a factor in reproduction, the data are insufficient for generalization, and as earlier workers also concluded, this analysis indicates no conclusive correlations between exposure and reproduction. It seems significant, however, that when advance reproduction is not present on cut-over areas, spruce and fir seedlings become established most readily on disturbed ground where the organic layers have been broken up and mineral soil is exposed. Conditions for the germination and survival of these seedlings in the forest and in the open, then, are quite different.

Dana (1930) summarized lumbering and forest management practices for all the Northeast. He discussed the spruce types of the region, and presented graphically (pages 32-33) counts of spruce and balsam fir as contrasted with hardwoods at various intervals after cutting. He showed that spruce and balsam fir easily maintain themselves in the spruce flat where the poorly drained soils are usually unfavorable to hardwoods. Hardwoods appear to increase after cutting in the spruce-hardwoods forest type, and perhaps also in the spruce slope type. The comparisons of spruce and balsam fir suggest that fir increases over spruce in the spruce flat (up to 40 years after lumbering) because of its more rapid growth upon release. It must therefore predominate at the next cutting. In the spruce-hardwood forest type, the spruce holds its own over fir because of its ability to compete with hardwoods. The thin soils of the spruce slopes are quite unfavorable to fir and here the spruce easily maintains its relative numbers.

A recent paper (Bowman, 1940) on the pulpwood forests in Michigan indicates that problems are similar there. It is concluded that recovery of spruce-fir forest is determined by the advance reproduction, its rate of growth and that of its associated species on the site. Lesser considerations are the degree of dominance of inferior species left after cutting and the tendency of shrubs to monopolize the site.

The Region

The northern section of Oxford County, Maine, where the Swift River watershed is located, is in the transition between the Canadian and the Upper Austral Regions (Merriam, 1898). The average frostless season is about 120 days, with late frosts occurring from about May 1 to June 10, and early frosts about October 1. Precipitation averages about 20-40 inches per year, with one-half to three-fourths of the total occurring between May 1 and October 1. The longest normal dry period during the average frostless season is 25 days. The precipitation-evaporation ratio for the average frostless season is 100 (Livingston and Shreve, 1921).

The region has been described as the New England Upland (Klimm, Starkey, and Hall, 1937). It varies from 1,000-2,000 feet above sea level, with mountains rising upwards of 3,000 feet throughout. Although the soil is practically unclassified througout northwestern Maine, the Swift River region has been mapped as rough and stony land (Marbut, 1935). Since the soils are

definitely podzolic, they are probably related to the widespread Hermon series of northern New England. The parent material is of glacial origin and slightly or non-calcareous. Thus the soils of forested areas are shallow podzols intermixed with boulders and ledges. Cursory examination permits the statement that the typical soil profile is similar to that described by Westveld (1931). Agricultural soils in northern Oxford County are commonly alluvial and restricted to the narrow valleys.

Gentle forested slopes are the outstanding characteristic of the topography of the region. In the uncleared valleys and less rolling land along stream courses, well-developed forests of considerable extent also occur. The steeper slopes of the mountains are generally covered with forest, but extensive ledges and a very rough land-surface give a broken aspect to the landscape.

Common and longstanding descriptive terms are locally applied to the forests occupying the lower and the upper slopes. The traditionally outstanding value of spruce and the tendency to think of hardwoods and fir as weed trees — conditions no longer accurate in fact — have led to the acceptance of a forest type classification in the spruce region based almost exclusively upon the occurrence of spruce (Hosmer, 1902; Murphy, 1917; Dana, 1930; Westveld, 1930, 1931). The names and descriptions given to the various topographically distinct forest types in the literature include: (1) *spruce swamp* — the forest of the lower, more poorly drained areas, composed principally of red and black spruce, balsam fir, tamarack, northern white cedar, soft maples and black ash; (2) *Spruce flats* — the forest of better-drained, moist soils along water courses where, in addition to spruce and balsam fir, an admixture of the maples, hemlock, white pine, and the birches may occur; (3) *mixed spruce-hardwood* — the forest of the benches and lower slopes of the mountains, with the deepest, richest forest soils of the region, where red spruce, balsam fir, sugar maple, beech, white and yellow birches predominate, and where normally the best tree growth of the region occurs; (4) *spruce slope* — the forest of the upper slopes, where the soil is thinner, stony, and with variable moisture content, composed of nearly pure stands of red spruce and balsam fir, with locally yellow and white birch trees scattered throughout; and (5) *old-field spruce* (called in the region pasture-spruce) communities which have established themselves on abandoned pasture or tillage lands and are usually composed of pure stands of spruce, red or white.

The above classification serves well enough for practical purposes in the second-growth forests of the Swift River Valley region, although it was actually based upon the original forests. From the viewpoint of the ecologist there is practically no precise information concerning the true nature of these spruce types except that described by foresters who have been primarily interested in the commercially valuable species only, and who have usually lumped the hardwoods together as such, and introduced a "weed-tree" category for the less valuable species (Westveld, 1931). The need for precise phytosociological analysis of the entire vegetational complex on each topographic area is obvious.

Methods

After cruising a large portion of the Swift River watershed and the immediately adjacent territory, a representative stand from each of the so-called spruce flat, mixed spruce-hardwood, spruce slope, and old-field spruce communities was selected for intensive sociological analysis. The stands selected were of as uniform age as could be found. They were stands concerning whose past history some records were available, and they were all located within a radius of 5 miles of Roxbury Village. All of the stands were so mature as to appear ready to cut for pulpwood, judging by the criteria commonly used in the region. No typical example of the spruce swamp forest was encountered in the survey, and consequently this study does not include an analysis of the forests of the extremely moist sites.

The method of sampling was essentially that described by Oosting and Billings (1939), with modifications as described by Oosting and Reed (1942) in their analysis of white birch communities in northern Oxford County. After the natural limits of each stand had been determined by a preliminary cruise, a series of 10 sets of quadrats was laid out. Following a compass the sets were spaced evenly at the widest possible intervals throughout the longest diameter of the stand. Each set of quadrats consisted of a nest of 3 quadrats, the largest size being 10 by 10 meters on a side, with the smaller sizes (4 by 4 meters and one square meter respectively) superimposed in one corner. On the largest plot, counts and diameters were obtained for all the woody individuals over one inch D.B.H., or over 10 feet tall. Records for over- and understory were kept separate. Shrubs and woody reproduction under one inch D.B.H., or less than 10 feet high were counted on the 4 by 4 meter plots. Records for the woody reproduction less than one foot high were kept separately from those for the one to ten foot height. Herbs were listed on the one square meter quadrats and their coverage estimated. From these data it was possible to derive intimate knowledge of each synusia, including density, and frequency of all woody plants as well as the basal area of the dominant and secondary trees in each stand. The frequency and average coverage of the herbaceous plants were also determined. Since the stands were essentially of the same age, it is possible to make direct comparisons of them layer by layer, and thus to establish their similarities and differences in quantitative as well as qualitative terms.

The Stands Selected and the Sites Described

For clarity the usual nomenclature will be applied to the various stands upon which this study is based. It is important to emphasize that all stands were so mature as to be considered ready for a pulpwood cut at the time this study was made. No two stands were more than 7 miles apart at their extremities, thus obviating climatic differences, other than those specifically ascribable to altitudinal variations.

Spruce Flat.—The stand in the spruce flat forest type was located along the westerly town line of Andover, Maine, adjacent to Horseshoe Brook. The

vegetation of this site had received the usual treatment of the local second-growth forests of the region. It had been repeatedly operated for several generations, the last cutting having occurred in 1924. Thus, the stand consisted of those trees too small to have been cut during the last lumbering operation, together with those which appeared after 1924. The average age of the dominants was 57 years. The general aspect was that of a mixed spruce-hardwood forest.

The site was approximately 700 feet above sea level and was more moist than the sites located at higher altitudes in the region. The surface of the ground was covered by a layer of litter about one-fourth inch thick, beneath which the fermentation layer averaged one-eighth to one-fourth inch in depth. A well-mixed humus and gray mineral mass lay next below, extending 3 to 4 inches downward to the uppermost part of the B horizon. The usual podzol profile of the region continued downward from 2½ to 4 feet where a gravelly sand of glacial origin represented the parent material. The slightly rolling topography of the area coupled with the underlying gravelly sand made for good drainage.

Mixed Spruce-Hardwood. — The stand selected as representative of the mixed spruce-hardwood forest type was in Byron, Maine, on Lot 11, Range 17. Operated heavily about 55 years ago this stand had had little disturbance in recent years. The average age of the dominants was found to be 53 years, with the conifers 10 years older than the hardwoods on the average. The name of this forest type truly describes the general appearance of the stand.

The site occurred on a moderate slope with a northwestern exposure at an elevation of approximately 1800 feet above sea level. Litter, one-eighth to one-fourth inch thick, covered a thin fermentation layer beneath which was about 4 inches of dark humus gradually grading into the gray layer of soil at the base of the A horizon. The shallow podzol profile was well exemplified beneath this stand. Numerous boulders occurred throughout the area although the surface of the land appeared relatively smooth.

Old Field Spruce.—The stand selected from the old field spruce forest type was also in Byron, Maine, on Lot 10, Range 17, immediately adjacent to the mixed spruce-hardwood stand. It had developed within the past 60 years for the area was known to have been in pasture about 50 years ago and some of the oldest trees were 58 years of age at the time of this study. The stand as a whole was typically uneven-aged indicating the random method of seedling establishment which characterizes the closing in of the poorer or the overgrazed pasture areas of the region. The average age of the very unevenly spaced dominants was found to be about 40 years. Frequent openings in the spruce canopy were typical and pure white birch dominance over areas of 1 to 3 acres was found in such openings at intervals throughout the stand. The openings also permitted persistence of densely stocked "islands" of young tree reproduction. The dominant conifers, although of good size and considered ready for cutting, were actually of relatively inferior quality, because of the many numerous low limbs which failed to self-prune.

The soil profile was typically podzolic except for the absence of a notice-

able amount of humus, and a very poorly developed fermentation layer. The site seemed to be somewhat drier than that of the adjacent mixed spruce-hardwoods, due undoubtedly to the deficiency of humus, and because of the presence of a more uniform gravel base beneath the B horizon.

Spruce Slope. — The stand selected to represent the spruce slope forest type was near the dome of Brush Mountain, Byron, Maine, at an approximate elevation of 2,700 feet above sea level, and about 2,000 feet above the Swift River Valley. The general area was typical of many of the "black-topped" mountains of the region. The stand itself extended upward from about 300 feet below the summit of the mountain, covering the surface of the dome on the north, south and west exposures, except for relatively small areas of exposed ledge. The trees were of an inferior quality because of their failure to self-prune, although the stand was closed except for the bare rock outcrops. The dominant trees were somewhat shorter than those of the same species at lower altitudes, but only those with direct exposure to the northwest showed evidence of distortion due to the prevailing winds. The stand itself appeared uniformly coniferous except for occasional white birch individuals. The trees were characteristically restricted in location to the small flat areas between the large boulders and ledges. In a few instances trees were observed to have been stunted as they grew in the more exposed situations with their only footholds in the crevices of the ledges.

The average age of the somewhat uneven-aged dominants was about 45 years. No evidence or records exist of this stand having been subjected to serious disturbance, since possible forest fires of the last century.

The site was definitely rougher and steeper than any of the others upon which this study is based. The soil was thin, even in the pockets between boulders and in the crevices on partially covered ledges. There was little of the typical gray material at the base of the A horizon. The litter layer was from 1 to 3 inches in depth over both the mineral soil and the margins of the otherwise exposed ledges throughout the stand. The fermentation layer was occasionally as much as one inch thick. The roots of the trees were heavily matted and superficial, due to the shallow soil and immediately underlying granite and gneiss.

The Vegetation of the Stands

DOMINANT TREE SPECIES

Phytographs of the dominant tree species[1] in each of the four forest types are presented in Fig. 1. Trees of only 4 to 6 species constituted the entire dominant layer in each representative stand. Of these red spruce and balsam fir were the only dominants present in all four types. The evidence from the dominant stratum alone reveals that four species, i.e., red spruce, balsam fir, red maple, and yellow birch were common to and important in both the stand from the spruce flat and from the mixed spruce-hardwood forests; whereas the old-field spruce and the spruce slope forests were fundamentally pure

[1] Nomenclature for arborescent species is that of Harlow, W. M. and E. S. Harrar, Textbook of Dendrology, 1941; for other species, Gray's Manual, 7th edition.

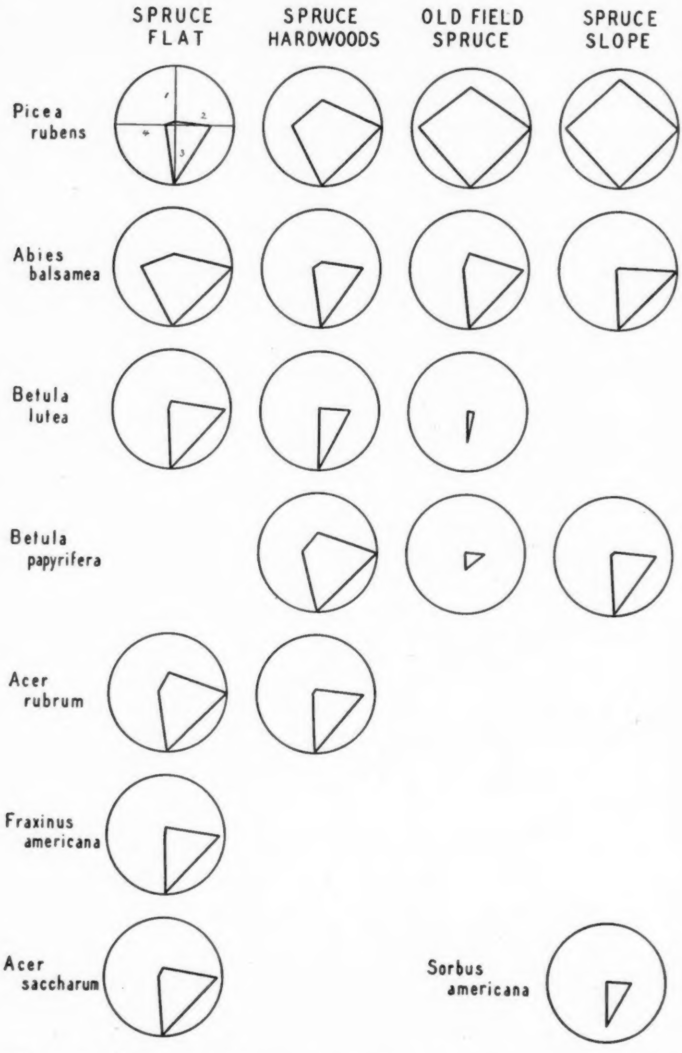

Fig. 1. Phytographs of the dominant tree species in the four types of forest. Radius 1, Percentage of total dominant abundance. Radius 2, Percentage frequency. Radius 3, Percentage of total size classes represented. Radius 4, Percentage of total dominant basal area. In these phytographs the inner end of each radius represents the absence of its assigned sociological characteristic. All phytographs based on ten 10 × 10 meter plots.

coniferous stands, with white birch the only dominant hardwood species common to both.

Comparing, now, the two stands from the mixed forests as tc the average number of dominant individuals (density) per 100 square meters, we find that the density of the deciduous species collectively was 15.1 in the spruce flat stand against 8.7 for the coniferous species, and in the mixed spruce-hardwood stand the density of deciduous species was 6.6, against 7.4 for the conifers By contrast, the old-field spruce and the spruce slope stands are represented on the same basis as follows: density of deciduous species in old-field spruce community 0.4, coniferous species 13.8; density of deciduous species in the spruce slope community 6.7, coniferous species 38.2. The average basal area of the dominants in square feet per 100 square meters in each stand was divided between the deciduous and the coniferous species thusly: spruce flat stand, deciduous species — 7.4; coniferous species 17.4; mixed spruce-hardwood stand, deciduous species — 15.5, coniferous species — 32.4; old-field spruce stand, deciduous species — 0.63, coniferous species — 53.0; and the spruce slope stand, deciduous species — 1.4, coniferous species 26.0 The total basal area of all dominants in square feet per 100 square meters was as follows: in the spruce flat stand, 26.9; in the mixed spruce-hardwood stand, 47.9; in the old-field spruce stand, 53.7; and in the spruce slope stand, 27.4.

Basal area computations are probably the best single criterion for evaluating each stand in terms of marketable pulpwood represented by the dominant trees. Table 1 shows the comparison of basal area among the dominant

TABLE 1.—Percent of the total dominant basal area by species in each of the four types of stands.

	Spruce Flat	Mixed Spruce-Hardwood	Old Field Spruce	Spruce Slope
Coniferous Species				
Picea rubens	16.1	52.8	89.0	90.5
Abies balsamea	53.9	13.6	9.8	4.2
All coniferous species	70.0	66.4	98.8	94.7
Deciduous Species				
Betula papyrifera	....	26.5	1.0	5.2
Betula lutea	4.1	0.8	0.2	....
Sorbus americana	....	....	....	0.1
Acer saccharum	8.5	....	....	....
Acer rubrum	17.2	6.3	....	....
Fraxinus americana	0.2	....	....	....
All deciduous species	30.0	33.6	1.2	5.3

species of each stand. The relative area of each dominant species may be seen as well as a comparison of all deciduous species with all coniferous species within each stand and among the four stands.

It is evident (Table 1) that these second-growth stands were better stocked with the two coniferous species, red spruce and balsam fir, than with any other commercially valuable species or group of species in the dominant stratum. It is apparent also that red spruce was represented by a much greater yield of wood than balsam fir within each stand except that of the spruce flat site, and that the typical second growth stand in each of the four habitats

studied would yield two-thirds or more of the most desirable pulpwood species regardless of its previous history.

SUBDOMINANT SPECIES

The frequency and density of the subdominant species in all four forest types are presented in Table 2. In this stratum spruce and balsam fir alone

TABLE 2.—Frequency and density of the subdominant woody species in the four types of stands. Based on ten 10 × 10 meter plots.

		Spruce Flat	Mixed Spruce-Hardwood	Old Field Spruce	Spruce Slope
Picea rubens	f	10	100	100	90
	d	0.4	3.2	3.4	5.8
Abies balsamea	f	80	30	90	50
	d	2.7	0.3	1.9	1.1
Betula papyrifera	f	10	30	....	80
	d	0.2	0.5	....	1.2
Acer rubrum	f	100	40		
	d	8.6	0.4		
Betula lutea	f	90	20		
	d	2.9	0.2		
Acer saccharum	f	20	10		
	d	4.6	0.3		
Acer spicatum	f	100			
	d	8.9			
Fraxinus americana	f	90			
	d	5.5			
Ostrya virginiana	f	50			
	d	3.0			
Acer pennsylvanicum	f	50			
	d	2.5			
Ilex verticillata	f	20			
	d	0.6			
Fagus grandifolia	f	20			
	d	0.4			
Tsuga canadensis	f	20			
	d	0.2			
Prunus pennsylvanicum	f	10			
	d	0.7			
Pinus strobus	f	10			
	d	0.3			
Populus tremuloides	f	10			
	d	0.1			
Corylus rostrata	f	90			
	d	8.4			
Alnus incana	f	40			
	d	6.9			
Hamamelis virginiana	f	30			
	d	2.3			
Amelanchier canadensis	f	20			
	d	0.5			
Viburnum cassinoides	f	20			
	d	0.4			
Cornus alternifolia	f	10			
	d	0.1			
Total	d	62.2	4.9	5.3	8.1

consistently occurred in all stands. As was true in the dominant layer, the subdominant species characteristic of the spruce-flat forest type and of the mixed spruce-hardwood type were genuine admixtures of hardwood and softwood species, whereas the secondary layers of the old field spruce and of the spruce slope types were almost exclusively made up of conifers. The number of subdominant species decreased from a maximum of 22 in the spruce flat stand, through 6 in the mixed spruce-hardwood type, and 3 in the spruce slope type, to only 2 in the old field spruce community.

It is significant that 16 of the 22 subdominant species of the spruce flat stand occurred on that site in the subdominant layer. Of these 16 species, 5 tree species, i.e., *Prunus pennsylvanicum, Fagus grandifolia, Pinus strobus, Tsuga canadensis,* and *Populus tremuloides,* were encountered on not more than 2 of the plots, and thus may be considered accidental species in this stand. Further, the fact that this lowland site favored height growth of several tall shrubs, i.e., *Corylus rostrata, Alnus incana, Hamamelis virginiana, Ilex verticillata, Viburnum cassinoides,* and *Cornus alternifolia,* made for their inclusion in this arbitrarily chosen size-class. The presence of these several accidental tree species, and tall shrubs, among the secondary trees of the stand is indicative of a competitive factor to the more valuable species which is unique for this stand among those upon which this study is based.

Since frequency and density alone do not indicate the entire sociological importance of the components of a community, Table 3 is included to show the basal area of the subdominant species in each stand.

TABLE 3.—The basal area of subdominant woody species in each of the four types of stands expressed as square feet per 100 square meters.

	Spruce Flat	Mixed Spruce-Hardwood	Old Field Spruce	Spruce Slope
Picea rubens	0.13	3.61	0.14	0.90
Abies balsamea	0.91	0.07	0.14	0.18
Betula papyrifera	0.02	0.35	......	0.13
Betula lutea	0.06	0.14		
Acer saccharum	1.50	0.02		
Acer rubrum	0.23	0.21		
Acer spicatum	0.95			
Fraxinus americana	0.68			
Corylus rostrata	0.84			
Acer pennsylvanicum	0.36			
Ostrya virginiana	0.52			
Alnus incana	1.17			
Hamamelis virginiana	0.23			
Ilex verticillata	0.10			
Amelianchier canadensis	0.10			
Viburnum cassinoides	0.04			
Prunus pennsylvanicum	0.07			
Fagus grandifolia	0.10			
Pinus strobus	0.05			
Cornus alternifolia	0.02			
Tsuga canadensis	0.15			
Populus tremuloides	0.01			
Total	8.24	4.40	0.28	1.21
Average	0.37	0.73	0.14	0.40

The relative basal area of red spruce and balsam fir in the secondary layer was in favor of red spruce within the mixed spruce-hardwood community and that of the spruce slope, with the reverse being true in the spruce flat stand. The intensive competition offered to the commercially valuable species of the spruce flat stand by the accidental species, the tall shrubs, and the weed tree species is further emphasized by the data of Table 3. For four such species, *Acer spicatum, Corylus rostrata, Ostrya virginiana,* and *Alnus incana* the average basal area per 100 square meters is greater than the average of all the species within the subdominant stratum. The relatively low frequency and density values of the hardwood species of the secondary layer within the mixed spruce-hardwood stand are coupled with very low basal area values.

TREE REPRODUCTION BENEATH THE SUBDOMINANT STRATUM

Frequency and density of the tree reproduction in the four forest types are shown in Table 4. As with the upper strata, there is a greater number of species represented by tree reproduction within the spruce flat and the mixed spruce-hardwood stands than in the other two communities. Spruce and balsam fir were the only two species found reproducing beneath each of the stands. Although white birch, yellow birch, mountain ash, and beech occur within the spruce slope and the old field spruce stands, their frequency values are not

TABLE 4.—Frequency and density of tree reproduction in the four types of stands. Based on ten 4 × 4 meter plots in each type. Over one foot includes all individuals 1-10 feet tall or one inch in diameter; under one foot, those less than one foot tall.

		Spruce flat		Spruce-hardwood		Old-field spruce		Spruce slope	
		over 1 ft.	under 1 ft.	over 1 ft.	under 1 ft.	over 1 ft.	under 1 ft.	over 1 ft.	under 1 ft.
Abies balsamea	f	80	100	60	100	20	90	50	30
	d	5.5	16.9	1.6	45.2	1.7	48.5	0.6	1.0
Picea rubens	f	......	30	20	80	20	90	70	70
	d		0.3	0.7	5.7	0.3	5.7	2.2	2.0
Acer rubrum	f	40	60	50	100	20	70	......	
	d	3.4	6.8	1.1	14.6	0.2	3.9		
Betula papyrifera	f	10	40	10	20			30	20
	d	0.1	0.6	0.2	0.9			0.5	0.3
Betula lutea	f	40	30	20	50		20		
	d	1.1	0.5	0.5	0.7		0.2		
Acer saccharum	f	90	80	80	100				
	d	4.9	5.2	3.8	5.9				
Sorbus americana	f	......	......	20	30		10	10	20
	d			0.2	0.4		0.1	0.2	0.2
Fraxinus americana	f	70	70						
	d	1.9	2.3						
Fagus grandifolia	f	......		30	60		10		
	d			0.4	1.2		0.1		
Acer pennsylvanicum	f	......	20	10	20				
	d		0.3	0.1	0.4				
Acer spicatum	f	40	60						
	d	0.8	1.3						
Populus tremuloides	f				10				
	d				0.2				
Total	d	16.7	34.2	8.6	75.2	2.2	58.5	3.5	3.5

greater than 30 percent in any instance and their average number (density) per 100 square meters is less than one. A significant quantity of red maple reproduction in the old field spruce stand was apparent.

In general, few species not already represented in the upper strata were found in the sapling or seedling stages in any of the stands. The relative significance of coniferous reproduction in each stand was directly comparable to the importance of those same conifers in the dominant and subdominant layers of the same stands. Sugar maple and red maple showed obvious importance in the spruce flat and in the spruce-hardwood stands. A singular feature of the tree reproduction in the spruce-hardwood stand was the presence of considerable beech. Mountain maple appeared exclusively in the spruce flat stand among plants of these size classes. The lack of reproductive capacity of white birch beneath any type of canopy was obvious.

Seedlings in a stand are always more abundant than saplings and almost invariably the number of seedlings of a species far exceeds that of the saplings. However, mortality rates are widely variable for species and in different stands. Balsam fir produces far more seedlings than any species in all four types of stands but the sapling counts indicate that 60-95 percent of these seedlings die, probably within the first few years of their lives. This is, of course, related to the relatively high light requirement of the species (Moore and Rogers, 1907; Zon, 1914). The number of spruce seedlings is more nearly comparable to that of hardwoods and the mortality between seedling and sapling sizes is likewise comparable. Although fir may comprise 50-80 percent of the total seedling count, its high mortality results in an equalizing of hardwood, spruce and fir numbers in the sapling sizes.

The greatest total number of seedlings is produced in the spruce-hardwood type where only 11.4 percent survive to the sapling stage (density 8.6). The numerous seedlings of the old-field spruce stands suffer even greater losses for only 3.7 prcent survive as saplings (density 2.2). In the spruce flat type sapling density (16.7) is about half (49%) that of seedlings. The spruce slope counts of saplings and seedlings are identical which, in terms of survival, supports Hosmer's (1902) contention that the moss duff cover is the best seed bed.

In general, all species show a reduction of individuals between seedling and sapling sizes but fir, red maple and spruce, in the order named, suffer by far the greatest losses. The number of seedlings of white birch in the spruce slope type and of yellow birch in the spruce flat is about half the number of saplings which suggests that, with increasing maturity, birch should become less important or disappear from these sites.

PLANTS OF THE FOREST FLOOR

Shrubs.—The frequency and density of the shrubs, less than 10 feet in height, or less than one inch in diameter, encountered in each of the four forest types are shown in Table 5. The paucity of shrubs in all stands except that of the spruce flat is evident. It appears that, with the possible exception

TABLE 5.—Frequency and density of the shrubs less than ten feet in height or less than one inch in diameter in the four types of stands. Based on ten 4 × 4 meter plots.

		Spruce Flat	Mixed Spruce-Hardwood	Old Field Spruce	Spruce Slope
Viburnum alnifolium	f	10	10		
	d	6.7	0.1		
Vaccinium pennsylvanicum	f	....	....		50
	d				0.5
Corylus rostrata	f	100			
	d	8.9			
Rubus allegheniensis	f	30			
	d	1.1			
Viburnum cassinoides	f	30			
	d	0.7			
Rubus triflorus	f	30			
	d	0.4			
Ilex verticillata	f	20			
	d	0.6			
Lonicera canadensis	f	20			
	d	0.2			
Cornus stolonifera	f	10			
	d	0.1			
Cornus alternifolia	f	10			
	d	0.1			

of *Corylus rostrata* in the spruce flat community, the low shrubs offer little competition to young tree reproduction in any of the stands. *Vaccinium pennsylvanicum* occurred on half of the 10 plots in the spruce slope stand, but was actually restricted in location to the most exposed niches where it appeared doubtful that conifer reproduction would yet be able to establish itself for want of sufficient soil. The utter absence of shrubs within the old-field spruce stand has no apparent explanation. The shrub population of the spruce flat community exhibits the same richness in number of individuals and of species as has been noted previously in all the higher strata of the forest.

Herbs.—The frequency and average coverage of the herbaceous vegetation of each of the forest types appears in Table 6. No herbs were encountered on the plots, nor seen within the entire spruce slope community. Lichens, liverworts, and mosses occurred abundantly and with regularity throughout the spruce slope stand, however. In all the other communities, some herbs were present, but only two species, namely *Maianthemum canadense* and *Aspidium spinulosum* variety *intermedium* were common to the spruce flat, mixed spruce-hardwood, and old-field spruce stands. As with all the woody species, the abundance of both individuals and species was markedly greater in the mixed communities of the spruce flat and mixed spruce-hardwood forests than where conifers occurred in nearly pure stands. It is not to be interpreted from the table that mosses, lichens, and liverworts are entirely absent from all communities except the spruce slope type, but rather that these cryptogams apparently take the place of the herbaceous flowering plants and ferns within that community.

On the basis of these limited observations and the data of Table 6, it

TABLE 6.—Frequency and coverage of herbs in the four types of stands. Based on ten 1 × 1 meter plots in each type.

		Spruce Flat	Mixed Spruce-Hardwood	Old Field Spruce	Spruce Slope
Maianthemum canadense	f	40	90	20	....
	c	2.0	10.6	0.6	
Aspidium spinulosum var.	f	30	60	10	....
intermedium	c	0.6	12.0	0.5	
Trientalis americana	f	80	30		
	c	1.9	1.6		
Clintonia borealis	f	20	40		
	c	0.6	4.7		
Lycopodium complanatum	f	....	....	10	....
var. *flabelliforme*	c			3.0	
Moss	f				50
	c	....	....	....	11.5
Liverwort	f	....	....	....	70
	c				10.5
Lichen	f	....	....	....	60
	c				10.5
Oxalis acetosella	f	....	80	....	....
	c		14.5		
Streptopus roseus	f	....	10	....	....
	c		0.5		
Medeola virginica	f	....	10	....	....
	c		0.5		
Osmunda claytoniana	f	....	10	....	....
	c		0.1		
Trillium erectum	f	....	10	....	....
	c		0.1		
Oakesia sessilifolia	f	70			
	c	2.3			
Cornus canadensis	f	70			
	c	3.0			
Aspidium noveboracense	f	40			
	c	4.0			
Lycopodium lucidulum	f	40			
	c	2.6			
Dalibarda repens	f	40			
	c	0.8			
Viola rotundifolia	f	30			
	c	1.5			
Aralia nudicaulis	f	30			
	c	0.7			
Phegopteris polypodioides	f	20			
	c	1.0			
Lycopodium obscurum	f	20			
	c	1.0			
Pyrola americana	f	20			
	c	0.6			
Tiarella cordifolia	f	20			
	c	0.2			
Pteris aquilina	f	10			
	c	0.5			
Coptis trifolia	f	10			
	c	0.5			
Carex sp.	f	10			
	c	0.5			

appears that the spruce flat community is characterized by an herbaceous complex very much like the Maianthemus-Cornus type[2] of the Adirondack Region of northern New York. Every characteristic species was found in our stand, namely, *Cornus canadensis, Maianthemum canadense, Aralia nudicaulis, Dalibarda repens, Trientalis americana,* and *Clintonia borealis.* Typical shrubs were also present, especially *Viburnum cassinoides* and *Amelanchier canadensis.* Site characteristics also agreed with Heimburger's descriptions.

Application of the Adirondack types to the remainder of the Maine stands indicates less close agreement than in the spruce flat community. The herbaceous complex of the mixed spruce-hardwood stand bore certain resemblance to the Oxalis-Cornus of the Adirondacks, but was entirely devoid of *Cornus canadensis.* The typical herbs actually present were *Oxalis acetosella, Clintonia borealis, Aspidium spinulosum* variety *intermedium, Medeola virginica, Trientalis americana,* and *Maianthemum canadense.* There was sufficient variation in the associated species, however, to indicate the necessity for more intensive investigation before accepting the Adirondack classification as synonymous with that occurring in northwestern Maine.

It seems quite impossible to draw any analogies between the ground cover of the spruce slope stand or the old-field stand and any of the herbaceous complexes hitherto described in the Northeast.

The Forest as a Whole

In spite of the variety of treatments which any portion may have suffered during the past 70 years, the Swift River watershed is characterized by only two physiognomically distinct types of pulpwood forests. Pure spruce forests continue to exist. Mixed spruce-hardwood forests occur widespread.

The occurrence of pure spruce communities is correlated directly with edaphic conditions. The steep, rocky, higher slopes of the mountains bear spruce in pure stand. The trees are rooted superficially over ledges and boulders which are barely covered with a litter layer and with only a few inches of mineral soil, showing no well-defined profile characteristics. Abandoned pasture lands may support pure spruce stands. Such lands were once cleared, then subjected to over-grazing and to an environment which destroyed the original humus layer through erosion, and finally abandoned as grazing areas. They are normally colonized, during and after grazing, in a quite random fashion by an uneven-aged stand of red spruce.

The mixed spruce-hardwood forests (spruce flat type and mixed spruce-hardwood type) occupy the more moist and less abused sites of the Watershed. It is beneath these communities that the more normal type of soil profile may be found in the region.

The role of red spruce in the entire forest of the Swift River region is noteworthy. In spite of habitat and regardless of the species complex in which

2 Reference to forest types as determined by herbaceous and shrub-like vegetation are to those of Heimburger (1934).

it is encountered, red spruce exhibits a remarkable adaptability to a wide variety of growing conditions. Among the dominants in all four types of stands, it was consistently present in the dominant, sub-dominant, and transgressive synusiae in every stand, indicating its ability to compete successfully with its associates throughout the life-span of the normal second-growth pulpwood forest. The total dominant basal area of red spruce was unsurpassed except in one instance by balsam fir in a single habitat (spruce flat). The role of red spruce as a pioneer species capable of persisting without interruption throughout the life span of a community is indicated in both the old-field spruce stand and in the spruce slope stand. In addition to these ecological attributes red spruce commands the highest price of all the pulpwood species in the region. It is, thus, a most significant species from every point of view.

Balsam fir, the other coniferous species most often associated with spruce in northwestern Maine, follows the general pattern of behavior noted by other workers in the Northeast (Moore and Rogers, 1907; Zon, 1914; Murphy, 1917; Moore, 1920; Dana, 1930). In our stands balsam fir was consistently present, but only in the spruce flat community did either its density or its total dominant basal area equal or surpass that of red spruce. Since the stands were as nearly mature as any pulpwood stands in the region may become before being cut, our results would agree with those of Moore and Rogers (1907) who indicated that they had observed the less tolerant fir to retard spruce on the more open areas of the Northeast only to decline in respect to spruce with advancing age because of early maturity and death of fir. However, in the spruce flat and mixed spruce-hardwoods stands in our region, balsam fir surpassed red spruce in both frequency and density among woody species less than 10 feet in height (Table 4). It appears that red spruce and balsam fir normally maintain themselves in a sociological equilibrium which may favor supremacy of spruce in terms of yield per acre on the drier sites, but which permits survival of both species in every segment of the forest studied.

The hardwoods are obviously important in the Swift River watershed only on the moister sites where well developed soil profiles exist. The relationship between moistness of site and development of hardwood species is well illustrated in every stand studied. By far the greatest variety of hardwood species and individuals appeared within the spruce flat community and the most limited representation occurred within the spruce slope community. That the hardwoods occupy a position of great ecological importance in both types of mixed stands (spruce flat and mixed spruce-hardwood) is indicated by the fact that their total dominant basal areas represented one-third of that of all species in both instances. The most severe competition between the hardwood and softwood species in the mixed forest types occurs among those individuals of the transgressive and seedling stages where sugar maple, yellow birch, beech, and ash may occur as associates. In the spruce flat forest some evidence exists that certain shrubs (hazelnut and alder) and small trees (striped maple and mountain maple) may temporarily be severe competitors with the valuable tree species of the subdominant layer.

The lesser plants of the forest communities form anomalous combinations

which can only be interpreted as the culmination of the varied treatment afforded each particular site studied. Some shrubby and herbaceous species survive logging and, thus, are found in the pioneer stages of the succeeding community, a fact previously noted in young birch stands in the same region (Oosting and Reed, 1942). Other lesser species fail to survive the removal of the mature forest and their places are taken by new complexes whose relationships are not revealed by this study. Edaphic and moisture conditions would seem to be controlling factors. The number of individuals and species of both shrubs and herbs in each habitat decreases directly as the site becomes drier, behaving exactly as the tree species in this respect. The poorly developed, or once-abused soils, of the pure coniferous stands support a negligible ground cover, practically devoid of shrubs and with mosses, lichens, and liverworts locally abundant. The spruce slope community is noteworthy for the complete absence of herbs.

To determine whether the two physiognomically different vegetation types of the Swift River region are distinct forest associations or whether only a single association exists, the species lists of all four second-growth stands were examined to establish the characteristic combination of species for the entire forest. The method is essentially that of Braun-Blanquet (1932). The characteristic combination of species is considered to include those whose degrees of fidelity fall in categories 5, 4, or 3; as well as those species which were present in at least three of the four types of communities studied.

Those species common to three of the four stands studied are listed and their occurrence is indicated in Table 7. Nine species are included in this table, all of which are, thus, to be used in determining the characteristic combination of species of the forest as a whole.

Those species determined to be exclusive to a single community (fidelity 5), those designated as selective (fidelity 4), and those classified as preferential (fidelity 3), are included in Table 8. Forty-eight species are included in this list, which combined with those species included in Table 7, constitute the characteristic combination of species for the forest as a whole.

The characteristic combination of species is then the summation of those listed in Table 7 and those listed in Table 8. This combination includes a

TABLE 7.—Species common to three of the four stands studied, and the community in which each is found.

	Spruce Flat	Mixed Spruce-Hardwood	Old Field Spruce	Spruce Slope
Abies balsamea	×	×	×	×
Betula lutea	×	×	×	×
Betula papyrifera	×	×	×	×
Picea rubens	×	×	×	×
Aspidium spinulosum var. *intermedium*	×	×		×
Acer rubrum	×	×		×
Fagus grandifolia	×	×		×
Maianthemum canadense	×	×		×
Sorbus americana		×	×	×

TABLE 8.—Species whose fidelity values fall in categories 3, 4, or 5, as revealed from a comparison of the species lists of all four types of forest communities studied.

Fidelity 5	Fidelity 4	Fidelity 3
Alnus incana	*Acer pennsylvanicum*	*Cornus canadensis*
Aspidium noveboracense	*Acer saccharum*	*Corylus rostrata*
Betula populifolia	*Acer spicatum*	*Viburnum alnifolium*
Cornus alternifolia	*Amelanchier canadensis*	
Cornus stolonifera	*Aralia nudicaulis*	
Dalibarda repens	*Carex* sp.	
Fraxinus americana	*Clintonia borealis*	
Hamamelis virginiana	*Coptis trifolia*	
Ilex verticillata	*Oakesia sessilifolia*	
Lonicera canadensis	*Populus tremuloides*	
Lycopodium clavatum	*Rubus allegheniensis*	
Lycopodium complanatum	*Trientalis americana*	
Lycopodium obscurum	*Viola rotundifolia*	
Medeola virginica		
Osmunda claytoniana		
Ostrya virginiana		
Oxalis acetosella		
Phegopteris polypodioides		
Pinus strobus		
Pteris aquilina		
Pyrola americana		
Ribes prostratum		
Rubus idaeus var. *aculeatissimus*		
Rubus triflorus		
Salix sp.		
Sambucus racemosus		
Streptopus roseus		
Tiarella cordifolia		
Trillium erectum		
Tsuga canadensis		
Vaccinium pennsylvanicum		
Viburnum cassinoides		

total of 57 species, and serves as a standard against which the species list of each community may be compared separately. The result of this comparison expressed in percent is the *coefficient of community*. This index has previously been applied to establishing the relationship between individual stands, and between each stand and the entire association of which it is a part (Braun-Blanquet, 1932). The more nearly the coefficient of community for the various stands approaches 100 percent, the more uniform and alike is the entire forest. Further, the comparison of each stand to a common standard provides a basis for contrasting one stand directly with another and arriving at a measurement of their floristic similarity.

The coefficient of community may be applied to individual stands to determine their relation to the entire community and the figures are presented in Table 9 which represent the comparative relationship of our stands to the characteristic combination of species of the forest as a whole.

The data in Table 9 clearly indicate that great variation exists between the pure coniferous forests and the mixed forests when each is evaluated

TABLE 9.—Determination of the coefficient of community. Standard includes 48 species of fidelity 3, 4, or 5 and 9 species common to three of the four stands studied, and the standard is equivalent to the characteristic combination of species.

Stand	Species in common with standard	Coefficient of community (per cent)
Spruce flat	45	78.9
Spruce-hardwood	37	64.9
Old-field spruce	11	19.3
Spruce slope	5	8.8

against the characteristic combination of species for the forest as a whole. It, thus, is apparent that floristically there is little justification for considering that a single forest association exists in the region. Further, the floristic nature of the stands clearly reflects their ecological as well as historical differences already established by field observation and the statistical analysis of the quadrats.

Of the pure coniferous forest the better floristic development of the community appears on the old-field site, whose soil profile is quite normal as compared to that of the spruce slope site, except for the absence of appreciable humus.

Between the two stands which include large numbers of hardwood species the floristic similarity is very close. The lower, moister site of the so-called spruce flat truly supports the most varied flora. That the term spruce flat is truly applicable to the second-growth forest of such sites in our region is highly questionable from these data or from a reconnaissance of a much wider area than that sampled in this study. Locally the term spruce flat continues to be applied to these mixed forest communities, but our results would suggest that structurally the forest occupying the lower portions of the topography might better be considered as a more mesophytic phase of the so-called mixed spruce-hardwood community which has long been recognized on the slopes of these mountains.

Discussion

Methods of cutting Maine forests have been controlled largely by demand and have consequently been selective in nature. Far-sighted foresters early became concerned over the future composition of these forests if selection of species were long continued. At various times studies have been initiated to determine the effects of selective cutting but usually new demands have resulted in new lumbering methods before soundly based silvicultural methods could be established. Now, the pulpwood industry uses almost all species and clear-cutting is a general practice. The future composition of pulpwood forests is therefore still somewhat problematical for clear-cut areas have in general not yet had time to produce mature stands nor to demonstrate their productiveness.

The stands upon which this report is based were selected because they

were representative of second-growth forests which had developed to mid-maturity on essentially clear-cut sites representing the usually recognized basis of type classification. The data on the composition of these stands should therefore furnish a basis for comparing present conditions with those of the past and likewise should be indicative of what may be expected after clear-cutting.

The reports of Cary (1894, 1896) include stand tables for virgin spruce slope and spruce-hardwood forest in Maine. Hosmer (1902) and Murphy (1917) give figures for uncut forest of the relative numbers of spruce and other species in the spruce slope type. Dana's (1930) generalized diagrams likewise add to the picture of virgin forest composition on spruce flat, spruce-hardwood and spruce slope sites. Although direct comparisons with these figures are not possible it is apparent that the originally recognized sites are still supporting forest communities which are probably as distinct as they ever were. However, certain changes in composition are likewise apparent.

Virgin spruce-slope forests, varying with site and altitude, contained in their overstory as few as 7 percent and up to 24 percent hardwoods. Fir constituted a small proportion (0.5-18 percent) of the stand. Our spruce slope values are therefore similar to virgin forest in every respect.

Virgin spruce-hardwood overstory was apparently about half spruce and half other species of which fir usually constituted a small proportion (2 percent) but might make up as much as 23 percent. Hemlock was locally an important constituent. Our sampling showed a reduction in numbers of spruce (40 percent) and no marked change in fir (15 percent) or hardwoods. Sugar maple and beech, characteristic in the overstory of virgin stands were replaced by red maple, which, being a successional species should be expected. Earlier reports of the composition of second growth spruce-hardwood include beech and sugar maple in the overstory but these individuals were undoubtedly relics of virgin conditions which would probably have been removed in the next cutting when hardwoods were in demand.

Considering the available descriptions of virgin forest conditions it would appear that, in the Swift River area, the types are maintaining themselves as distinctly as before cutting began. Certain changes in composition have taken place, in that balsam fir has probably increased somewhat at the expense of spruce on all sites. This may reasonably be considered as related to the relative immaturity of the stands as compared to virgin forest. The proportion of hardwoods has increased somewhat on spruce flat and spruce-hardwood sites and certain incidental species (arbor vitae, hemlock), never of great abundance nor present with high frequency values, have nearly disappeared. Red maple, essentially a successional species, is far more abundant than in earlier days in the forest of the lower altitudes.

These generalizations apply to forests which through the years have been subject to the usual sequence of unplanned selective cuttings, and now have appeared following the first so-called clear cutting. Our evidence does not indicate any radical change in future stand composition for spruce slope, spruce-hardwood or spruce flat sites after clear cutting.

The probability is that clear cutting will maintain the present vegetation complexes more satisfactorily than any form of selective or diameter limit method. Linn (1918) and McCarthy (1919) emphasized that the number of hardwoods increases following diameter-limit and other forms of selective cutting and likewise that, in spite of their release by the selective cut, the softwoods remaining do not sufficiently increase their increment in growth to pay for the selection. Clear cutting simplifies the logging operation, reduces the cost (Linn, 1918) and likewise eliminates losses through blowdown. Under these circumstances it would seem that clear cutting should become a general practice. Certain qualifications should be added to this generalization, however, in the light of modern ecological and silvical information. Stands should not be cut until trees of the predominating species have passed the peak of their growth rates, and then only if the advance reproduction of conifers assures a quick establishment and early development of the next stand (Westveld, 1931). Under these conditions no concern need be given for seed trees and thus about the only argument for leaving culls standing is eliminated. Churchill (1927) and Cary (1928) have shown the economic feasibility of girdling wolf trees. There is no ecological or silvical justification for leaving them. With their elimination the new stands would be almost even-aged, of uniform growth throughout, and all the land would contribute to new growth.

Modern cutting practices in the Swift River region will undoubtedly perpetuate the mixed forest and probably favor its development on all sites except those recently retired from pasturage or on those thin-soiled areas high in the mountains where hardwoods appear unable to compete with the more adaptable red spruce. Although our data indicate that balsam fir is more abundant in pulpwood forests than it was in virgin stands there is no evidence that there will be further increases at the expense of spruce. There is likewise, no indication that red spruce and balsam fir are disappearing completely from pulpwood lands. With the proper concern for advance growth at the time of cutting and the insurance of an adequate seed source, it appears that red spruce and balsam fir will constitute at least half of the yield of pulpwood per acre on every type studied.

Summary

1. The extensive forests of Maine are almost entirely second-growth resulting from a sequence of changing lumbering operations that have continued from about 1800 to the present.

2. Except for the clearing for agriculture, cutting was decidedly selective until relatively recently. The lumber market demanded first white pine and then spruce. Paper mills then created a demand for pulpwood which began with spruce, progressed to fir, and finally expanded to include hardwoods. Most stands will thus have been selectively cut several times and have now, or soon will be, clear-cut. Under these changing conditions it is obvious why silvical or ecological principles have been given little consideration.

3. Studies bearing on planned silviculture have all been made within the past 45 years and, because of the recent general adoption of clear cutting, only

a few contribute materially. Purely ecological studies of the pulpwood forests are even fewer than silvical ones. No detailed phytosociological analyses of Maine pulpwood forests are available.

4. The forests of the Swift River region in Oxford County, Maine, are typical of vast acreages throughout the state. Here, after a general reconnaissance, representative stands of spruce slope, mixed spruce-hardwoods, spruce flat, and old-field spruce were selected and studied intensively in the summer of 1940.

5. Each stand was analyzed qualitatively and quantitatively by a series of quadrats for dominant and subdominant trees, reproduction of trees, shrubs, and herbs. Frequency, density and basal area were determined for woody individuals and frequency and coverage for herbs. In addition, observations of soil profiles were recorded.

6. The important species of the dominant stratum in the spruce flat and spruce hardwood stands were red spruce and balsam fir with a mixture of hardwoods including red and sugar maple, yellow birch and ash in the former and white birch, yellow birch and red maple in the latter. In the essentially coniferous spruce slope and old-field stands red spruce and balsam fir made up most of the overstory with scattered paper birch. Yellow birch was also present in the old-field and mountain ash in the spruce slope.

7. In the subdominant stratum only spruce and fir consistently occurred in all stands. The spruce flat and spruce-hardwoods had additionally a mixture of numerous hardwoods, 22 and 6 species respectively, but the spruce slope and old-field subordinate individuals were almost exclusively conifers.

8. Analysis of the sapling and seedling strata of tree reproduction indicated no radical changes to be expected in the generalizations made for the composition of strata of tree size.

9. Except for occasional plants of *Viburnum alnifolium* in the spruce-hardwoods and *Vaccinium pennsylvanicum* in the spruce slope, shrubs were absent in all stands except the spruce flat. Of the nine species recorded here only hobble-bush and hazel nut occurred in significant numbers.

10. Herbs were most abundant in species and numbers in the spruce flat and spruce-hardwoods stands. Under the coniferous cover of old-field spruce three species were found and none were observed in the spruce slope. The complex of herb species in the spruce flat is apparently similar to the Cornus-Maianthemum forest type of the Adirondacks. The other three communities showed insufficient agreement with Heimburger's forest types to permit their application in Maine without further study.

11. Floristically two types of pulpwood communities exist in the Swift River region, namely, pure coniferous forests on the abandoned agricultural lands and high on the slopes of the mountains, and mixed spruce-hardwood forests on the lower slopes and along the better drained watercourses of the lowlands.

12. From this study, it seems that the practice of clear cutting will serve better than any other type of lumbering to preserve the forest of this region relatively unchanged in type and composition.

REFERENCES

BOWMAN, A. B. 1940—Growth on cutover spruce-fir plupwood lands in northern Michigan. Paps. Mich. Acad. Sci. **26**:123-133.

BRAUN-BLANQUET, J. 1932—Plant Sociology. (Trans. by G. D. Fuller and H. S. Conard). New York. 439 pp.

CARY, A. 1894—On the growth of spruce. Ann. Rep. Forest Commiss. State of Maine **2**:14-102.

———1896—Report of Austin Cary (in) Ann. Rep. Forest Commiss. State of Maine **3**:15-203.

———1907—Practical forestry on a spruce tract in Maine. U. S. D. A. Forest Serv. Circ. **131**. 15 pp.

———1928—The hardwood problem in the Northeast. Jour. For. **26**:865-870.

CHURCHILL, H. L. 1927—Girdling of hardwoods to release young conifers. Jour. For. **25**:708-714.

DANA, S. T. 1930—Timber growing and logging practice in the Northeast. U.S.D.A. Tech. Bull. **166**. 112 pp.

HEIMBURGER, C. C. 1934—Forest-type studies in the Adirondack region. Cornell Univ. Agr. Exp. Stat. Mem. **165**. 122 pp.

HOSMER, R. S. 1902—A study of the Maine spruce. Ann. Rep. Forest Commiss. State of Maine **4**:65-108.

KLIMM, L. F., STARKEY, O. P., AND N. F. HALL. 1937—Introductory economic geography. New York. 492 pp.

LINN, E. R. 1918—Silvical systems in spruce in northern New Hampshire. Jour. For. **16**:897-908.

LIVINGSTON, B. E. AND F. SHREVE. 1921—The distribution of vegetation in the United States as related to climatic conditions. C. I. W. Publ. **284**. 585 pp.

MARBUT, C. F. 1935—Soils of the United States. U.S.D.A. Atlas of American Agriculture, Pt. 3.

McCARTHY, E. F. 1919—Observations on unburned cut-over lands in the Adirondacks. Jour. For. **17**:386-397.

MERRIAM, C. H. 1898—Life zones and crop zones of the United States. U.S.D.A. Bull. **10**.

MOORE, B. 1920—Humus and root systems in certain northeastern forests in relation to reproduction and competition. Jour. For. **20**:233-254.

———1926—Influence of certain soil and light conditions on the establishment of reproduction in northeastern conifers. Ecology **7**:191-220.

——— AND R. L. ROGERS. 1907—Notes on balsam fir. Forest. Quart. **5**:41-50.

MURPHY, L. S. 1917—The red spruce: its growth and management. U.S.D.A. Bull. **544**. 100 pp.

OAK, C. E. 1894—Foreword. Ann. Rep. Forest Comm. State of Maine **2**:1-14.

OOSTING, H. J. AND W. D. BILLINGS. 1939—Edapho-vegetational relations in Ravenel's woods, a virgin hemlock forest near Highlands, North Carolina. Am. Midl. Nat. **22**:333-350.

——— AND J. F. REED. 1942—The establishment of a white birch community on cut-over pulpwood land in northwestern Maine. Bull. Torr. Bot. Cl. **69**:647-661.

WESTVELD, M. 1930—Suggestions for the management of spruce stands in the Northeast. U.S.D.A. Circ. **134**. 23 pp.

———1931—Reproduction on pulpwood lands in the Northeast. U.S.D.A. Tech. Bull. **223**. 52 pp.

ZON, R. 1914—Balsam fir. U.S.D.A. Bull. **55**. 68 pp.

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The Minor Genus Polemoniella

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In the course of a recent review of the content of the genus *Polemonium,*[1] several names which had been proposed under that genus were dismissed from consideration on the ground that they belonged to *Polemoniella.* Discussion of this genus is accordingly called for.

The first recognized member of this group was named *Polemonium micranthum* by Bentham.[2] When Gray[3] revised the *Polemoniaceae* in 1870 he divided the genus *Polemonium* into three sections on the basis of corolla and filament characters, his third section comprising only this one species. Peter[4] raised these sections to subgenus rank and gave them names, the third becoming *Polemoniastrum.* In 1904 Heller[5] noted the striking difference in aspect between this species and the typical Polemoniums, and proposed the genus *Polemoniella* for it. Brand[6] returned to Gray's view that only the sectional segregation is desirable. In the writer's opinion the differences are sufficient to justify Heller's creation of a new genus, as brought out by the following key:

DURATION perennial or exceptionally biennial; flowers rarely solitary, usually grouped in cymes aggregated into a compound inflorescence; peduncles mostly axillary to reduced leaves or entire bracts; flowers showy, the corolla exceeding the calyx; stamens elongate and styles usually exserted beyond them, favoring cross-pollination........*Polemonium*

DURATION annual, ephemeral; flowers solitary or in clusters of 2 to 6; peduncles or pedicels mostly borne opposite the petiole-bases of moderately reduced leaves; flowers inconspicuous, the white corolla equalling or shorter than the calyx; stamens short and styles about equalling them, favoring self-pollination..*Polemoniella*

The latter genus comprises a single western-North American species and an uncertain number of southern-South American ones, five different names, one under *Polemonium* and four under *Gilia,* having been proposed for material from there. These were distributed by Brand[6] between two *Polemoniums,* transferred by Nelson and Macbride[7] to *Polemoniella,* and reduced by Borsini[8] to a single *Polemonium.*

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1 Amer. Midl. Nat. **27**:741, 1942.
2 In DC. Prodr. **9**:318, 1845.
3 Proc. Amer. Acad. Arts Sci. **8**:280. 1870.
4 In Engl. & Prantl Pflanzenf. **4(3a)**:51, 1891.
5 Muhlenbergia **1**:57, 1904.
6 In Engler's Pflanzenr. IV.**250**:30, 1907.
7 Bot. Gaz. **61**:35, 1916.
8 De Lilloa **8**:201, 1942.

Polemoniella Heller

Plants small ephemeral annuals. Leaves alternate, pinnate. Inflorescences lateral or terminal on branches, consisting of solitary or clustered flowers (up to 6). Peduncles or pedicels mostly borne opposite the petiole-bases of moderately reduced leaves. Flowers inconspicuous; sepals foliaceous and accrescent, united about $^{1}/_{3}$ their length into a campanulate calyx; petals white, united half their length, the free part oblong, terminally obtuse and erose, equalling or shorter than the calyx. Androecium of 5 slightly irregular stamens, their filaments basally adnate to the corolla-tube, all shorter than the corolla. Gynoecium of 3 united carpels, the styles short, their free stigmatic tips lying in the midst of the anthers.

Key to Species

RANGE northwest-North American; leaflets up to 13 per leaf; flowers more often solitary than clustered; filaments adnate to the tube $^{1}/_{4}$ their length, basally dilated and more or less pilose.................*P. micrantha*

RANGE southern-South American; leaflets up to 11 per leaf; flowers more often clustered than solitary; filaments adnate to the tube about half their length, no basal dilation or pilosity being evident..........*P. antarctica*

POLEMONIELLA MICRANTHA (Bentham) Heller, loc. cit.

Polemonium micranthum Benth. in DC. Prodr. **9**:318, 1845.

TYPE: Columbia valley, Washington; *Douglas.*

This little annual grows in grassland, open thickets, and weedy places at 1000 to 5000 feet altitude. It is native to western North America, from central California east to Utah, and north to southern British Columbia and western Montana. Its seeds may get mingled with those of grasses grown commercially in Oregon, and a specimen perhaps arising from such a source was collected near Milton, Massachusetts. (Herb. N. E. Bot. Club).

It varies in stature, extent of branching, size of leaflets, etc., but this is so obviously connected with the moisture or nutrient content of the soil that no attempt to separate it into infraspecific entities seems desirable.

POLEMONIELLA ANTARCTICA (Grisebach) Nelson & Macbride, loc. cit.

Polemonium antarcticum Griseb. Abh. Akad. Wiss. Göttingen **6**:131, 1854.

TYPE: Cabo Negro, Brunswick Peninsula, Chile; *Lechler* No. 1000.

The South American member of the group is recorded to grow in semiarid grassland and scrub in the foothills and in the mountains up to 3000 feet altitude in southern Chile and Argentina. Besides the original, four other occurrences of it have received species names, and since these are all based on different type specimens, they require some recognition. Consideration of their features suggests that they do not deserve higher status than forma, so their names are herewith appropriately combined.

Forma **typica** Wherry,[1] nomen novum.

The original Grisebach plant may first of all be named forma *typica*. It is characterized by having the leaflets "obovate-subrotund and spatulate," the flowers rather remote and mostly solitary, and the calyx exceeding the corolla, the lobes of which are erosely 2-notched. Other forms are now listed in alphabetical order.

Forma **arcuata** (Hieronymus) Wherry, stat. nov.

Gilia arcuata Hieron., Bol. Acad. Nac. Cordoba **3**:367, 1879.

TYPE: Santa Cruz valley, Argentina.

This differs from the typical form in lanceolate subacute leaflets, cymose flowers (3 or even 6 altogether), corolla barely exceeding the calyx, its lobes denticulate.

Forma **diffusa** (Philippi) Wherry, stat. nov.

Gilia diffusa Phil., Linnaea **30**:187, 1859 (August, acc. to Brand).
Polemonium gayanum (Wedd.) Brand, loc. cit., in part.

TYPE: Santiago, Chile.

Characterized by having the leaflets oblong and acute, the flower-bearing branches corymbose-grouped, and the corolla about equalling the calyx.

Forma **gayana** (Weddell) Wherry, stat. nov.

Gilia gayana Wedd. Chlor. and. **2**:82, 1859 (June acc. to Brand).
Polemonium gayanum (Wedd.) Brand in Engler's Pflanzenr. IV.**250**:46, 1907.
Polemoniella "*gayanum*" Nels. & Macbr. Bot. Gaz. **61**:35, 1916.

TYPE: Santiago, Chile.

Described as having the leaflets linear-lanceolate and acute, the flowers in groups of 2 or 3, and the corolla equal to the calyx.

Forma **johowi** (Meigen) Wherry, stat. nov.

Gilia johowi Meigen, Engl. Bot. Jahresb. **17**:291, 1893. (Volume erroneously given as 16 in Brand and the Index Kewensis.)
Polemonium gayanum (Wedd.) Brand, in part.

TYPE: Santiago, Chile.

The describer of this entity recognized its variability in that he characterized the leaflets as "oval to longish-lanceolate, pointed to almost rounded." He further noted that "each shoot terminates in a flower" as well as what is here considered a genus character, namely that the flowers arise opposite petiole-bases.

[1] In spite of the statement in the International Rules of Botanical Nomenclature (1930), Art. 46, that in the interest of accuracy, completeness, and ease in verification "it is necessary to cite the author who first published the name in question," some recent writers have urged that when the epithet "*typica*" or an equivalent is proposed, no author-citation is called for. The resulting necessity of attributing such names to "Anon." would seem to oppose the aims stated.

Forma **violascens** (Spegazzini ex Brand) Wherry, comb. nov.

Polemonium antarcticum f. *violascens* Speg. ex Brand in Engler's Pflanzenr. IV. **250**:46, 1907.

Polemonium gayanum var. *violascens* Brand, loc. cit. (mistakenly cited by Borsini, De Lilloa **8**:202, 1942, as "Speg. ex Brand.")

TYPE: Rio Senguer, southern Argentina; *Spegazzini.*

Recorded by Brand as differing from his *Polemonium gayanum* only in having violet-tinged herbage. Such development of anthocyan is occasional in plants which chance to grow in especially sterile situations, as the collector noted for this, so deserves only the status of forma.

These five forms are assigned to a single species for the following reasons: Brand considered an entity, *Polemonium gayanum,* with "linear-lanceolate" leaflets to be characteristic of more northern latitudes — about 32 to 37° — and one, *P. antarcticum,* with "ovate" leaflets to range from latitude 50° southward into Tierra del Fuego. These ranges are connected, however, by specimens cited by Borsini, and the correlation of leaflet-shape with geography fails to hold anyway. Meigen's *Gilia johowi* from Santiago, in the northern area, was definitely stated to have in part oval leaflets; while Borsini figured a specimen from Tierra del Fuego with leaflets essentially linear-lanceolate. There is also no correlation between inflorescence-complexity and range as implied in Brand's text-descriptions, both solitary and cluster-flowered plants being recorded from northern and southern localities alike. No confirmation of the differences in seed-characters noted by Brand has been practicable. The herbarium material available indicates variation in individual areas to exceed the supposed diagnostic criteria.

The distinctive features of these several named forms, according to the original descriptions and (as to seeds) Brand's data, are as follows; other combinations of characters can be found in herbarium material, but seem unworthy of further naming:

KEY TO FORMS OF POLEMONIELLA ANTARCTICA

FLOWERS in part solitary; corolla shorter than calyx.
- LEAFLETS rounded; seeds (according to Brand) black and mucilaginous when wet .... *typica*
- LEAFLETS varying from rounded to lanceolate; seeds brown and spirilliferous when wet .... *johowi*

FLOWERS all clustered; corolla about equal calyx.
- INFLORESCENCES seemingly corymbose: leaflets oblong, acute .... *diffusa*
- INFLORESCENCES cymose; leaflets lanceolate, acute.
  - CYMES 3- to 6-flowered .... *arcuata*
  - CYMES 2- to 3-flowered; seeds brown, spirilliferous.
    - HERBAGE green or slightly bronzed .... *gayana*
    - HERBAGE strongly bronzed .... *violascens*

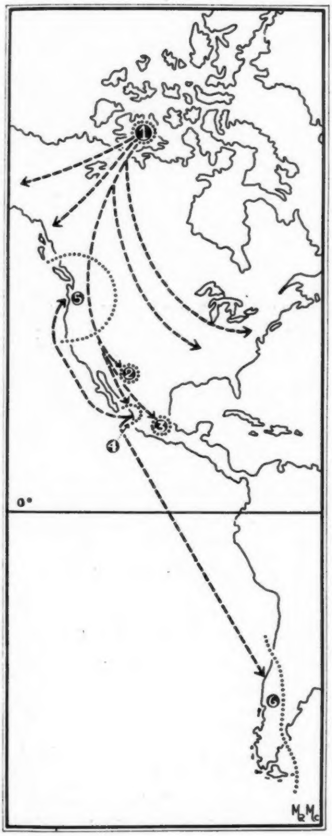

Fig. 1. Range of *Polemoniella.* The numbers mark notable areas: 1. ?Ancestot, of *Polemonium.* 2. *Polemonium pauciflorum.* 3. *Polemonium mexicanum.* 4. ?Anumbers mark notable areas: 1. ?Ancestor *micrantha.* 6. *Polemoniella antarctica.*

While this genus has undoubtedly been derived from the circumboreal *Polemonium,* no present-day member of that group can be recognized as a direct ancestor. Significant tendencies are shown, however, by two species which developed toward the southern end of the genus-range: in northern Mexico and adjacent Arizona and Texas, *P. pauciflorum,* having the inflorescence reduced (but corolla elongate); and in central Mexico, *P. mexicanum,* having the duration reduced and corolla shortened (but calyx specialized). Presumably in what is now western Mexico, at some time during the Tertiary, an entity developed in which the trends named first under each of these were combined (but the parenthesized ones failed to develop); and this gave rise to *Polemoniella,* intermediate stages becoming extinct.

Representatives of the newly formed genus no doubt migrated out in various directions, but subsequent geological or climatic changes exterminated all but two which chanced to reach remote refuges: *P. micranthum,* Oregon and neighboring states, and *P. antarcticum,* southern Chile and Argentina. How the latter got across to southern South America can not be decided; but as representatives of many genera show a similar bifocal range, there must have been some late-Tertiary land-route with elevations high enough to evade tropical conditions at the equator. The present case can be added to those noted by Du Rietz[1] in his recent discussion of bifocal ranges.

1 Acta Phytogr. Suecica **13**:215, 1940.

Review of the Genera Collomia and Gymnosteris

Edgar T. Wherry

For identification of miscellaneous collections of *Polemoniaceae,* the writer has found published keys more or less unsatisfactory, so has reviewed the relationships in several groups. The results attained in *Polemonium* and *Polemoniella* have already been published in this journal.[1] Studies of two additional genera are now placed on record.

In the family *Polemoniaceae,* only the subtropical and Andean genera, — *Bonplandia, Cantua, Cobaea,* and *Huthia* — are well differentiated. The temperate genera show interconnection through one or more species combining genus-characters. If complete dissociation is demanded as a requisite for generic independence, there can here be little if any subdivision of the family. This was realized by Kuntze,[2] who planned to place every member of the remaining genera in the single genus *Polemonium,* though he never got around to completing the project. A somewhat more liberal attitude, favored by some present-day workers, is to recognize three genera, with leaf-characters as the primary basis for separation, as follows:

Key to Widespread Polemoniaceae on the Three-genus Plan

LEAVES pinnately compound, alternate; calyx herbaceous................*Polemonium*

LEAVES entire, lobed, or dissected but rarely pinnately compound; calyx only exceptionally herbaceous throughout.

LEAF-POSITION opposite or exceptionally alternate, the margins entire or essentially so; flowers salverform, showy..*Phlox*

LEAF-POSITION alternate or exceptionally opposite, the margins only rarely entire; flowers various...*Gilia*

The first two of these genera are fairly homogeneous, but the third is so utterly polymorphic that its maintenance as a unit leads to more confusion than clarity. One interloper into this super-genus *Gilia* has already been treated elsewhere:[3] *Microsteris,* which was dumped into the gilioid melting-pot by Hooker, who, though an eminent taxonomist, never fully comprehended the relationships among the members of the *Polemoniaceae.* That this entity belongs closer to *Phlox* was clearly shown by Greene.[4] Nevertheless it was returned to *Gilia* by Brand,[5] who in his monograph showed at times keen discrimination but again great confusion.

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1 Amer. Midl. Nat. **27**:741, 1942; **31**:211, 1944.
2 Rev. Gen. Pl. **3**(2):202, 1898.
3 Brittonia **5**:60, 1943.
4 Pittonia **1**:141, 1887.
5 In Engler's Pflanzenreich IV.**250**:88, 1907.

Collomia

The principal refugee from *Gilia* discussed here is *Collomia* Nuttall.[1] This was accepted as a genus for many years after its proposal, though with varying species content. In his early treatment, Gray[2] considered its principal characters to be unequal stamens and mucilaginous seeds; he included 11 species, more than half of which are now regarded as belonging elsewhere. In the first edition of the Synoptical Flora, this author[3] introduced no essential changes. Continuing his studying and naming of additional species under *Gilia,* however, he changed his viewpoint, thus:[4]

"It has at length become evident that the unequal insertion of the stamens (so characteristic of *Phlox*) will no longer serve to distinguish *Collomia* from *Gilia*. Transitions occur in the same species from very unequal to equal insertion, or nearer to equality than in some other Gilias besides those of the Navarretia section. The character of solitary ovules having also failed, nothing remains but to remand Nuttall's genus *Collomia* to the already large and much diversified genus *Gilia*."

Carrying this viewpoint to its logical conclusion, Gray[5] then created a section *Collomia* of the genus *Gilia* to comprise the plants in question.

In 1887 Greene[6] called attention to a point missed by Hooker, Bentham, and Gray, namely that in the *Polemoniaceae* "by the calyx alone, especially as it appears not in flower, but in its after developments, in and of itself and in its relation to the fruit, we may limit and define good acceptable genera." He did make too sweeping general statements, such as that *Collomia,* as redefined, is "restricted to species well at agreement in habit" and that its calyx-segments are "perfectly equal." Nevertheless he did bring out a distinction between *Collomia* and *Gilia* sufficient to justify their maintenance as independent genera: in the former the tissue uniting the sepals is uniform with them in texture and upwardly plicate; in the latter the junction-tissue is membranous and non-plicate.

Greene's view was accepted by Peter,[7] by Brand,[8] and by the majority of subsequent compilers of floras and manuals. On the other hand, Gray's reduction of *Collomia* to a section of Gilia was followed by the editors of the 6th and 7th editions of his Manual, and by a few individual workers. The present writer is in full accord with Greene as to the usefulness of calyx-characters for generic segregation.

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1 Gen. N. Am. Pl. **1**:126, 1818.
2 Proc. Amer. Acad. Arts Sci. **8**:258, 1870.
3 Syn. Flora N. A. **2**(1):134, 1878.
4 Proc. Amer. Acad. Arts Sci. **17**:223, 1882.
5 Syn. Flora N. A., ed. 2, **1**(2) & **2**(1) Suppl.: 407, 1886.
6 Pittonia **1**:121, 1887.
7 In Engler & Prantl Pflanzenfamilien **4**(3a):48, 1891.
8 In Engler's Pflanzenreich IV.**250**:47, 1907.

GENUS ASSIGNMENTS

Collomia Nuttall Gen. N. Am. Pl. 1: 126, 1818; type species *C. linearis* Nutt. or (Cav.) Nutt.; cf. discussion below.

Courtoisia Reichenbach Cat. Hort. Dresden 1829 ex Icon. Bot. Exot. 3: 4, 1829; type "C. daucifolia" Reichb. =*Collomia heterophylla* (D.) Hk.

Cullomia Jussieu Dict. Sci. Nat. 42: 307, 1826; an obvious misprint.

Curtoisia Endlicher Gen. Pl. Suppl. 2: 60, 1842; another misprint.

Gilia Ruiz & Pavon Prodr. Fl. Peruv. Chil.: 25, 1794; expanded to include "G. heterophylla" by Douglas ex Hooker =*Collomia heterophylla* Hook.; and emended to include all species of *Collomia* by Gray Proc. Amer. Acad. Arts Sci. 17: 223, 1882.

Gymnosteris Greene Pittonia 3: 303, 1898, a genus created to comprise the entity named "Collomia nudicaulis" by Hooker & Arnott.

Hoitzia Jussieu Gen. Pl.: 136, 1789; expanded to include "Phlox linearis" Cav. and "Collomia linearis" Nutt. as "H. linearis" by Sprengel Syst. Veg. (ed. 16) 1: 626, 1825.

Myotoca Grisebach Abh. Akad. Wiss. Göttingen 6: 129 (repr. 41), 1854; noted as having been used in annotating specimens [of *Microsteris*].

Navarretia Ruiz & Pavon Prodr. Fl. Peruv. Chil.: 20, 1794; expanded to include *Collomia heterophylla* (Dougl.) Hook. by Bentham in DC. Prodr. 9: 309, 1845; and emended to include all species of *Collomia* by Kuntze Rev. Gen. Pl. 1/2: 432, 1891.

Phloganthea "Cav." ex Peter in Engl. & Prantl Pflanzenf. 4.3a: 48, 1891.

Phlox L. Sp.: 151, 1753; expanded to include "P. biflora" by Ruiz & Pavon Fl. Peruv. Chil. 2: 17, 1799, and "P. linearis" by Cavanilles Icon. Descr. Pl. 6: 17, pl. 527, 1801; both are species of *Collomia.*

Polemonium L. 1735 ex Kuntze Rev. Gen. Pl. 3(2): 202, 1898.

SECTION ASSIGNMENTS

Collomia Gray Syn. Fl. N. A. (ed. 2) 1(2) & 2(1) Suppl.: 407, 1886; proposed as a section of *Gilia* to include most species of *Collomia.*

Collomiastrum Brand in Engl. Pflanzenr. IV.250: 52, 1907; proposed to comprise *C. debilis* (Wats.) Greene and related species.

Courtoisia Reichenbach Icon. Bot. Exot. 3: 4, 1829, as "subgenus;" made by Gray Syn. Fl. N. A. (ed. 2) 1(2) & 2(1) Suppl.:408, 1886, a section under *Gilia.* Here made *Collomia* § **Courtoisia** (Reichb.) Wherry, comb. nov. Comprises *Collomia heterophylla* (Dougl.) Hook. and relative.

Eucollomia Bentham in DC. Prodr. 9: 307, 1845; proposed to comprise the original *C. linearis* Nutt. and related species.

Gilioides Bentham op. cit.: 308; included species now regarded as belonging to the genera *Gilia* and *Microsteris.*

Myotoca Grisebach Abh. Akad. Wiss. Göttingen 6: 129 (repr. 41), 1854; proposed for species now placed in *Microsteris.*

Phloganthea Gray Proc. Amer. Acad. Arts Sci. 8: 260, 1870; four Gilias.
Picracolla Nuttall J. Acad. Nat. Sci. Phila. (2) 1: 159, 1848; a *Gilia*.

Before taking up the species of *Collomia*, the vexing nomenclatorial problem involved in the type species of the genus requires discussion.

First, there were two South American entities described under the genus *Phlox:* "P. biflora" Ruiz & Pavon Fl. Peruv. Chil. 2: 17, 1799; and "P. linearis" Cavanilles Icon. Descr. Pl. 6: 17, pl. 527, 1801. Some workers have held these to be identical, but their diagnoses indicate considerable differences to exist between them.

Then came the work of Nuttall Gen. N. Am. Pl. 1: 126, 1818. He proposed the name *Collomia* for "a genus appertaining to the Natural Order POLEMONIDEAE and intermediate with *Phlox* and *Polemonium*." Under this was placed a single species, *C. linearis;* but following its diagnosis came the line: "*Phlox linearis* ? Cavan. ic. 6. p. 17. t. 527." The features of the entity Nuttall had in mind were then given in detail, with the locality "Near the banks of the Missouri, about the confluence of Shian [Cheyenne] river, and in the vicinity of the Arikaree village." Finally, Nuttall added: "It appears to be the same plant figured by Cavanilles, and first discovered in Chili. . . . To this genus probably also belongs *Phlox biflora* of Chili, which is also annual, but the habit appears to be different."

Today no one questions that both South American entities belong to *Collomia;* and they have even been considered specifically identical.

Unfortunately, differences of opinion now arise as to the validity of Nuttall's action and the epithets to be used for the entities involved. One viewpoint is that since Nuttall, when he erected the genus *Collomia,* associated the species epithet *linearis* with a North American plant, that epithet is not valid for the entity to which it had earlier been applied under another genus, even when this latter entity proves also to belong to the genus *Collomia.* This was the view held, in their monographic treatments, by Bentham, Gray, and Brand, and correspondingly accepted by the majority of compilers of manuals, floras, etc. Under it "Phlox linearis" Cavanilles, when transferred to *Collomia,* must be assigned the next earliest species epithet in the literature for the same plant: *Collomia cavanillesii* Hooker & Arnott Bot. Beechey's Voy. pt. 1: 37, 1830.[1]

The alternative view is that the species epithet *linearis* belongs to the entity to which it was originally applied, no matter what genus transfers may be made. This was urged by Philippi Anal. Univ. Chile 90: 217, 1895; under it the North American entity would have to bear the name "C. parviflora" Hooker in Curt. Bot. Mag. 56: pl. 2893, 1829. Feeling disinclined to sponsor a plan which would require complete reannotation of and republication upon North American material, the writer accepts the first view.

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1 The date of publication of part 1 is taken to be 1830 because it was abstracted in Linnaea 6, Litt. Ber. 155, which appeared in that year; some writers have given it as 1831.

An annotated list of the epithets which have been proposed in the genus *Collomia* is now given. The plan of presentation is the same as that of the writer's paper on *Polemonium*, above cited. As there, bold-face type signifies a novelty, italic an epithet already in the literature which is here accepted, and light-face roman a rejected name or combination. Brand's monograph is abbreviated to "Pol." and Kuntze's renamings to "Nav. Ktze." Species epithets are systematically decapitalized.

NAMES PROPOSED IN THE GENUS COLLOMIA

aggregata (Pursh) Porter apud Rothrock Rept. U. S. Geogr. Surv. w. 100° 6: 198, 1878; "Nav." Ktze. Belongs to the genus *Ipomopsis* (or *Gilia*).

aristella (Gray) Rydberg Mem. N. Y. Bot. Gard. 1: 318, 1900. In the course of revision of the *Polemoniaceae*, Gray Proc. Amer. Acad. Arts Sci. 8: 259, 1870, came upon an entity which seemed to agree with the description of *C. tinctoria* Kellogg Proc. Calif. Acad. Sci. 3: 17, 1863, but to intergrade with *C. linearis* Nutt. It was accordingly named "C. linearis var. subulata" Gray. Later, on reducing *Collomia* to a section of *Gilia*, Gray Syn. Fl. N. A. (ed. 2) 1(2) & 2(1) Suppl.: 408, 1886, decided to make it a species, and ignoring the Kellogg epithet renamed it "Gilia aristella." This became "Nav." Ktze. Then Rydberg loc. cit. put it back, as "C. aristella." Finally Brand Pol.: 51, 1907, rightly returned to Kellogg's prior species epithet, and transferred "var. subulata" to that. The difference being entirely a matter of vegetative development, this is reduced to the status of forms on a subsequent page. The epithet "aristella" is, then, to be discarded as a synonym.

atacamensis Philippi Anal. Univ. Chile 90: 217, 1895. This was well characterized by Brand Pol.: 54, 1907, as a highly dubious species. The features ascribed to it, leaves with terminal aristate lobes and calyx-lobes reflexed, indicate that if it is a member of the *Polemoniaceae* at all, it belongs under *Gilia*.

bellidifolia Douglas ex Hooker Fl. Bor. Amer. 2: 76, 1838. A *Microsteris*.

biflora (Ruiz & Pavon) Brand Engl. Bot. Jahrb. 36: 72, 1905, emend. Wherry; "Nav." & "Pol." Ktze.; "Gilia biflora" Macbride Contr. Gray Herb. 3(56): 57, 1918. This epithet is accepted for a South American species, "Phlox biflora" R. & P. Fl. Peruv. Chil. 2: 17, 1799, described as having the flowers "ex divisionibus caulis et ex axillis superiorum foliorum, bini, pedunculati . . . Corolla purpureo-caerulea." This entity was placed by Bentham in DC. Prodr. 9: 308, 1845, in synonymy under "C. coccinea Lehm.-Benth." in Edw. Bot. Reg. 19: pl. 1622, 1833. The latter is, however, a highly dissimilar species, with subsessile flowers in dense terminal clusters and red corollas. (Bentham was not invariably right in his interpretations of inter-relationships among the members of the *Polemoniaceae*.) In making the correct combination, Brand loc. cit. accepted Bentham's views as to the equivalence of the two. Several years ago, when a specimen from the Krukoff collection was submitted for

identification, the writer De Lilloa 5:368, 1940, reported its name as "Collomia biflora" [sensu Brand]. Subsequent consideration of the matter has led, however, to a change in viewpoint: it is now held that the combination *Collomia biflora* should be restricted to the entity to which the species epithet was originally applied, — a plant with violet flowers borne chiefly in 2-flowered clusters in stem forks and upper leaf-axils. Under this interpretation, the Krukoff specimen should bear the name *C. cavanillesii* Hooker & Arnott, as discussed below.

biflora var. erythraeoides (Grisebach) Brand Pol. : 50, 1907. Now regarded as a *Microsteris*, for reasons presented under "C. erythraeoides."

biflora var. lateritia (Don) Brand, loc. cit. Here considered a form of *C. cavanillesii* Hooker & Arnott.

cavanillesiana Don Gen. Hist. Dichl. Pl. 4: 247, 1838. A Mexican *Gilia*, the valid name for which is *G. pinnata* (Cav.) Brand Pol.: 112, 1907.

cavanillesii Hooker & Arnott Bot. Beechey's Voy. pt. 1: 37, 1830. Under the usual plan of straightening out the nomenclatorial mixup created by Nuttall when he established the genus *Collomia*, as above discussed, this is the valid epithet for the entity originally named "Phlox linearis" Cavanilles Icon. Descr. Pl. 6: 17, pl. 527, 1801. Workers who prefer a stricter interpretation of the rule of priority, however, will replace it by "Collomia linearis" (Cav.) Nutt. Gen. 1: 126, 1818.

chubutensis Spegazzini Rev. Agron. La Plata 1897: 619 ex Brand Pol. :89, 1907. Apparently a *Microsteris*.

coccinea Anon. Del. Sem. Hort. Hamburg 1832: 7; authorship attributed to Lehmann by Lindley (with a Latin diagnosis by Bentham) in Edw. Bot. Reg. 19: pl. 1622, 1833. It should therefore be cited as "C. coccinea Lehm. ex Lindl." As already noted, Brand Pol.: 50, 1907, reduced "C. coccinea" to synonymy under *C. biflora*, but this is not accepted here. Instead, the valid name for the species involved is taken to be *C. cavanillesii* Hook. & Arn., and the present entity is regarded as belonging under that as: *C. cavanillesii* **f. coccinea** (Lehm. ex Lindl.) Wherry, stat. nov. Differing from the typical form in having broadly lanceolate leaves coarse-toothed toward the tip, and bracted inflorescence.[1]

coccinea *β* parviflora Bentham in DC. Prodr. 9: 308, 1845. This was proposed to replace "C. lateritia" Don in Sweet Brit. Fl. Gard. 6: 206, 1833. The latter epithet is further discussed below.

debilis (Watson) Greene Pittonia 1: 127, 1887; "Gilia debilis" Watson Amer. Nat. 7: 302, 1873; "Nav." Ktze. A well-marked though variable species.

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1 As already stated, the writer prefers to follow priority as to correct classification rather than as to epithet, and in the text makes combinations accordingly. On the basis of priority of epithet, the correct combination in this case would be: "C. linearis" (Cav.) Nutt. **f. coccinea** (Lehm. ex Lindl.) W., stat. nov.

debilis var. camporum Payson Univ. Wyo. Publ. Bot. 1: 83, 1924. Since this differs from the original representative of the species in only minor respects, it is here made *C. debilis* ssp. *typica* **f. camporum** (Pays.) Wherry, stat. nov. Leaves entire and acutish.

debilis var. integra Payson loc. cit.; "C. hurdlei var. integra" Nelson Am. J. Bot. 18: 435, 1931. Differing from the typical form of ssp. *trifida* only in having fewer leaves trifid, this deserves only to be: *C. debilis* ssp. *trifida* **f. integra** (Pays.) Wherry, stat. nov. Many leaves entire; stamens included.

debilis var. ipomoea Payson op. cit.: 82. This entity is morphologically distinct and occupies a limited area at the eastern edge of the species range. It is therefore here made *C. debilis* **ssp. ipomoea** (Pays.) Wherry, stat. nov. Differs from ssp. *typica* in the larger, rose-pink flowers.

debilis var. larseni (Gray) Brand Pol.: 52, 1907; "Gilia larseni" Gray Proc. Amer. Acad. Arts Sci. 11: 84, 1876; "G. debilis var. larseni" Macbride Contr. Gray Herb. 3(56):57, 1918; *C. larseni* Payson Univ. Wyo. Publ. Bot. 1: 85, 1924. The last is here accepted.

debilis var. trifida Payson op. cit.: 85; "C. hurdlei var. trifida" Nelson Am. J. Bot. 18: 435, 1931. Regarded as primitive in its group, this is here made *C. debilis* **ssp. trifida** (Pays.) Wherry, stat. nov. The typical form has many leaves trifid; stamens included.

debilis var. typica Payson op. cit.: 81. In accordance with the usage as to categories preferred here, this becomes *C. debilis* **ssp. typica** (Pays.) Wherry, stat. nov. Flowers moderate-sized; stamens exserted.

diversifolia Greene Pittonia 1: 128, 1887; "Nav." Ktze. A segregate from *C. heterophylla* (Dougl.) Hook., perhaps deserving only subspecies status, but here kept distinct because of the much larger calyx, — around 12 mm. long at maturity. The original description gave the locality as in Colusa, the label on the type sheet in Lake County, Calif.

dulcis Lindley Rev. Hort. 19: 225, 1847. A misprint for *Collania dulcis*.

eritrichoides Grisebach Abh. Akad. Wiss. Göttingen 6: 130 (repr. 42), 1854; "Nav." Ktze. Evidently a *Microsteris*.

erythraeoides Grisebach loc. cit.; "Nav." Ktze.; "C. biflora var. erythraeoides" Brand Pol.: 50, 1907. The describer of this realized that it is not a typical *Collomia*, placing it, together with the preceding entity, in his "Section Myotoca." Its features of eglandular pubescence, opposite leaves, sparse flowers, and spreading calyx-lobes are those of a *Microsteris*, so Brand's allocation of it is not here accepted.

gilioides Bentham in Edw. Bot. Reg. 19: pl. 1622, p. 4, 1833; "Nav." Ktze. Acceptably made *Gilia gilioides* by Greene Erythea 1: 93, 1893.

gilioides var. glutinosa (Benth.) Gray Proc. Amer. Acad. Arts Sci. 8: 260, 1870. A *Gilia,* closely related to the next-preceding.

giliopsis Smyth Trans. Kans. Acad. Sci. 14: 133, 1896. Not only is this a misprint for "gilioides," but also presumably a misidentification, in that the *Gilia* involved is far-western.

glutinosa Bentham in Edw. Bot. Reg. 19: pl. 1622, p. 4, 1833. First made a variety of "C. gilioides" Bentham and later *Gilia glutinosa* (Benth.) Gray Syn. Fl. N. A. (ed. 2) 1(2) & 2(1) Suppl.: 408, 1886.

gracilis Douglas ex Hooker in Curt. Bot. Mag. 56: pl. 2924, 1829; successively assigned to the genera *Gilia, Phlox, Navarretia,* and *Polemonium;* and finally made the type of the independent genus *Microsteris* Greene Pittonia 3: 300, 1898, which is here regarded as preferable.

gracilis β andicola Bentham in DC. Prodr. 9: 308, 1845.

gracilis var. humilior Hooker Fl. Bor. Amer. 2: 76, 1838.

gracilis var. minuartioides Franchet Bot. Cape Horn: 356, 1889. These three entities are likewise classed as belonging to *Microsteris.*

grandiflora Douglas ex Lindley in Edw. Bot. Reg. 14: pl. 1166, note, 1828; fuller description ibid. pl. 1174; "Gilia grandiflora" Gray Proc. Amer. Acad. Arts Sci. 17: 223, 1882; "Nav." Ktze. A well-marked but rather variable species, next to *C. linearis* the most widespread.

grandiflora var. axillaris Nelson Bot. Gaz. 52: 270, 1911; "Gilia grandiflora var. axillaris" Macbride Contr. Gray Herb. 3(56): 57, 1918. A growth-form, here made *C. grandiflora* **f. axillaris** (Nels.) Wherry, stat. nov. Differs in having short fertile branches in many leaf-axils.

grandiflora var. cryptantha Regel ex Gray Proc. Amer. Acad. Arts Sci. 8: 259, 1870. The original place of publication has not been traced; Gray gave no data whatever. Judging from the varietal epithet, a variant with anomalously small flowers is represented, which may preferably be known as *C. grandiflora* **f. cryptantha** (Regel) Wherry, stat. nov.

grandiflora diffusa (Mulford) Piper Contr. U. S. Nat. Herb. 11: 465, 1906; "Gilia grandiflora var. diffusa" Mulford Bot. Gaz. 19: 120, 1894. This is like f. *axillaris* (Nels.) W. except that the lower branches are elongate, so made *C. grandiflora* **f. diffusa** (Mulf.) Wherry, stat. nov.

grandiflora β tenuiflora Bentham in DC. Prodr. 9: 308, 1845. A recombination of this minor variant is here proposed: *C. grandiflora* **f. tenuiflora** (Benth.) Wherry, stat. nov. Differing from the typical form in having a more slender corolla-tube and smaller limb.

heterophylla Hooker in Curt. Bot. Mag. 56: pl. 2895, 1829; "Gilia heterophylla" Douglas ex Hook. loc. cit.; "Courtoisia daucifolia" Reichenbach Cat. Hort. Dresden 1829 ex Icon. Bot. Exot. 3: X & 4, 1829; "C. bipinnatifida" Reichb. ibid pl. 208; "Navarretia heterophylla" Bentham in DC. Prodr. 9: 309, 1845; also sometimes confused with the Mexican "Gilia Sessei" Don Gen. Syst. Dichl. Pl. 4: 245, 1838. A highly distinct species; its typical form was 30 to 45 cm. high. Rather smaller was *C. heterophylla* **f. daucifolia** (Reichb.) Wherry, stat. nov.

howardi Jones Zoe 2: 250, 1891. Reduced by Payson Univ. Wyo. Publ. Bot. 1: 81, 1924, to synonymy with *C. debilis*, but here made *C. debilis* ssp. *typica* **f. howardi** (Jones) Wherry, stat. nov. Differs from the typical form in having the calyx 6 mm. but the corolla 25 mm. long.

humilis Douglas ex Hooker Fl. Bor. Amer. 2: 76, 1838; "C. gracilis β humilior" Hook. loc. cit.; *Microsteris humilis* Greene Pittonia 3: 301, 1898; also variously assigned under *Gilia*. Greene's view is accepted.

hurdlei Nelson Am. J. Bot. 18: 435, 1931. This is not here regarded as sufficiently distinct to deserve specific independence, so is made *C. debilis* ssp. *trifida* **f. hurdlei** (Nels.) Wherry, stat. nov. Said to differ in its leaves being sordid and entire.

hurdlei var. integra (Payson) Nelson loc. cit.; "C. debilis var. integra" Pays. Univ. Wyo. Contr. Bot. 1: 83, 1924; *C. debilis* ssp. *trifida* f. *integra* (Pays.) W., supra.

hurdlei var. trifida (Payson) Nelson loc. cit.; "C. debilis var. trifida" Pays. op. cit.: 85, cited by Nelson as "debelis var. integra;" *C. debilis* ssp. *trifida* (Pays.) W., supra.

lanceolata Greene ex Brand in Engl. Bot. Jahrb. 36: 72, 1905. Overlooking the earlier "C. parviflora" Hooker in Curt. Bot. Mag. 56: pl. 2893, 1829, Brand urged that Greene's ms. epithet might well replace "C. linearis" Nuttall. Here a different disposal is made: *C. linearis* Nutt. **f. lanceolata** (Greene ex Brand) Wherry, stat. nov. Lectotype, the sheet of Baker No. 138 in Greene's herbarium. Leaves lanceolate.[1]

larseni (Gray) Payson Univ. Wyo. Publ. Bot. 1: 85, 1924; "Gilia larseni" Gray Proc. Amer. Acad. Arts Sci. 11: 84, 1876; "C. debilis var. larsenii" Brand Pol.: 52, 1907; "Gilia debilis var. larseni" Macbride Contr. Gray Herb. 3 (56): 57, 1918. Accepted as a species.

lateritia Don in Sweet Brit. Fl. Gard. 6 (ser. 2, 3): pl. 206, 1833; "C. biflora var. lateritia" Brand Pol.: 50, 1907. Here regarded as *C. cavanillesii* Hook. & Arn. **f. lateritia** (Don) Wherry, stat. nov. Differs from the typical form in its short, broad corolla-tube and clavate stigmas.[2]

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1 Or alternatively "C. parviflora" Hook. **f. lanceolata** (Greene ex Brand) Wherry, stat. nov.

2 Or "C. linearis" (Cav.) Nutt. **f. lateritia** (Don) Wherry, stat. nov.

leptalea Gray Proc. Amer. Acad. Arts Sci. 8: 261, 1870. Made equivalent to "Gilia capillaris" Kellogg by Gray ibid. 17: 223, 1882; and acceptably named *G. leptalea* by Greene Erythea 4: 58, 1896.

linearis Nuttall Gen. N. Am. Pl. 1: 126, 1818; "Hoitzia linearis" Sprengel Syst. Veg. (ed. 16) 1: 626, 1825; "Gilia linearis" Gray Proc. Amer. Acad. Arts Sci. 17: 223, 1882; "Nav." Ktze. The complex nomenclatorial question here involved has been discussed above. Hooker was apparently the first to recognize the difficulty; he favored dropping the disputed epithet, and proposed "C. parviflora" Hook. in Curt. Bot. Mag. 56: pl. 2893, 1829, to replace *C. linearis* Nutt. for the North American entity. The writer retains Nuttall's epithet in its time-honored sense.

linearis (Cavanilles) Nuttall Gen. N. Am. Pl. 1: 126, 1818, as to epithet but not as to plant; "Phlox linearis" Cavanilles Icon. Descr. Pl. 6: 17, pl. 527, 1801; "Hoitzia linearis" Sprengel Syst. Veg. (ed. 16) 1: 626, 1825. The plan of dropping the disputed epithet resulted in *C. cavanillesii* Hooker & Arnott Bot. Beechey's Voy. pt. 1: 37, 1830, for the South American entity. That the rules of nomenclature require the retention of the epithet "linearis" for this was urged by Philippi Anal. Univ. Chile 90: 217, 1895.

linearis var. boulderensis Daniels Flora Boulder Colo.: 198, 1911. Here reduced to *C. linearis* Nutt. **f. boulderensis** (Dan.) Wherry, stat. nov. A variant with narrow, sharp-pointed leaves and bracts.[1]

linearis var. congesta Lunell Am. Midl. Nat. 4: 512, 1916. Here regarded as *C. linearis* Nutt. **f. congesta** (Lun.) Wherry, stat. nov. Stem branched.[1]

linearis var. humilis Brand Pol.: 49, 1907. Also recombined, to: *C. linearis* Nutt. **f. humilis** (Brand) Wherry, stat. nov. Low and branched.[1]

linearis var. picta Lunell Bull. Leeds Herb. (No. 2): 7, 1908. This may similarly become *C. linearis* Nutt. **f. picta** (Lun.) Wherry, stat. nov.[1] A variant with bronzed bracts.

linearis var. subulata Gray Proc. Amer. Acad. Arts Sci. 8: 259, 1870; *C. tinctoria* Kellogg Proc. Calif. Acad. Sci. 3: 17, 1863, "ex char." Gray; "C. tinctoria var. subulata" Brand Pol.: 52, 1907; "Gilia elmeri" Piper ms. ex Brand. This is here made *C. tinctoria* **f. subulata** (Gray) Wherry stat. nov. Stem much branched.

linoides Nuttall J. Acad. Nat. Sci. Phila. (2) 1: 159, 1848. Now regarded as a variant of *Gilia minutiflora* Bentham.

longiflora (Torrey) Gray Proc. Amer. Acad. Arts Sci. 8: 261, 1870. This has been assigned to various genera, but is usually classed as a *Gilia*.

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1 Or alternatively "C. parviflora" Hook. **formae boulderensis** (Dan.) Wherry, **congesta** (Lun.) W., **humilis** (Brand) W., and **picta** (Lun.) W., respectively.

macrocalyx Leiberg ex Brand in Fedde Rep. Sp. nov. 17: 317, 1921. A fairly distinct, narrowly endemic, species. Brand contrasted it with *C. debilis,* but it is much closer to *C. tinctoria.*

mazama Coville Proc. Biol. Soc. Wash. 11: 35, 1897; "Gilia mazama" Nelson & Macbride Bot. Gaz. 61: 34, 1916. Highly distinct and closely endemic.

micrantha Kellogg Proc. Calif. Acad. Sci. 3: 18, 1863. Placed in *Microsteris* by Greene Pittonia 3: 303, 1898. It differs in only minor respects from *M. humilis* (Dougl. ex Hook.) Greene.

myotica Grisebach ex Ind. Kew. 1: 585, 1893. This apparently represents both a mis-spelling and a misinterpretation: Grisebach Abh. Akad. Wiss. Göttingen 6: 129 (repr. 41), 1854, noted that he had used "Myotoca" as a genus epithet in annotating plants collected by Philippi, but actually published only "Collomia Nutt. Sect. Myotoca." The two species he included are believed to belong to the genus *Microsteris.*

navarretia Don Gen. Syst. Dichl. Pl. 4: 247, 1838. Now regarded as a member of the genus *Navarretia.*

nudicaulis Hooker & Arnott Bot. Beechey's Voy.: 368, 1841; "Nav." Ktze. This was made the basis of the genus *Gymnosteris* Greene Pittonia 3: 303, 1898. It will be discussed in the second part of this paper.

parviflora Hooker in Curt. Bot. Mag. 56: pl. 2893, 1829. Proposed as a substitute for *C. linearis* Nutt. Actually, if "C. linearis" (Cav.) Nutt. is accepted for the South American entity, Hooker's epithet is to be used for the North American one.

patagonica Spegazzini Rev. Agron. La Plata 1897: 550 ex Brand Pol.: 54, 1907. Recognized to represent a species of *Nicotiana.*

pringlei (Gray) Peter in Engl. Pflanzenf. 4(3a): 48, 1891; *Gilia pringlei* Gray Proc. Amer. Acad. Arts Sci. 21: 401, 1886. The latter holds.

pusilla Dusén Erg. Svensk. Exp. Magellansl. 3: 135, pl. 11, 1900. Subsequently realized to be an *Androsace.*

rawsoniana Greene Pittonia 1: 221, 1888; "Gilia rawsoniana" Macbride Contr. Gray Herb. 3(no. 56): 57, 1918. The largest known species of *Collomia,* endemic in a small area in south-central California.

scabra Greene Lflts. Bot. Obs. Crit. 2: 88, 1910. A segregate not here regarded as deserving higher status than *C. grandiflora* **f. scabra** (Greene) Wherry, stat. nov. A rough-hairy, short-leaved desert growth-form.

setosa Sieber ex Steudel Nom. Bot. (ed. 2) 1: 398, 1840. Apparently an independent proposal of the genus-name "Collomia," to contain an entity now generally recognized to belong to the genus *Felicia.*

sinistra (Jones) Brand Pol.: 54, 1907; "Gilia sinister" Jones Contr. W. Bot. 10: 57, 1902. The description shows this to be a *Gilia*.

söhrensi Philippi Anal. Univ. Chile 90: 218, 1895. Classed by Brand Pol.: 50, 1907, as equivalent to his "C. biflora var. lateritia," but here regarded as *C. cavanillesii* **f. soehrensi** (Phil.) Wherry, stat. nov. A branched form.[1]

stenosiphon Kunze Linnaea 24: 228, 1851; "Nav." Ktze. Placed by Brand Pol.: 50, 1907, in synonymy under "*C. biflora*," but here classed as *C. cavanillesii* **f. stenosiphon** (Kunze) Wherry, stat. nov. Differing from the typical form and f. *lateritia* in the corolla-tube being relatively short and slender.[1]

tenella Gray Proc. Amer. Acad. Arts Sci. 8: 259, 1870; "Gilia leptotes" Gray ibid. 17: 223, 1882; "Nav." Ktze.; "Gilia tenella" Nelson & Macbride Bot. Gaz. 61: 34, 1916; not *G. tenella* Bentham Pl. Hartw.: 325, 1849. Here regarded as a well-marked species of *Collomia*.

thurberi Gray Proc. Amer. Acad. Arts Sci. 8: 261, 1870; *Gilia thurberi* Gray ibid. 17: 223, 1882; "Nav." Ktze. Transfer to *Gilia* acceptable.

tinctoria Kellogg Proc. Calif. Acad. Sci. 3: 17, fig. 2, 1863; "C. linearis Nutt. var. subulata" Gray Proc. Amer. Acad. Arts Sci. 8: 259, 1870, as to a branched form; "Gilia tinctoria" Kellogg ex Curran, Bull. Calif. Acad. Sci. 1(3): 142, 1885; "Gilia aristella" Gray Syn. Fl. N. A. (ed. 2) 1(2) & 2(1) Suppl.: 408, 1886; "C. aristella" Rydberg Mem. N. Y. Bot. Gard. 1: 318, 1900. The original form was dwarf and unbranched.

tinctoria var. subulata (Gray) Brand Pol.: 52, 1907; "C. linearis Nutt. var. subulata" Gray Proc. Amer. Acad. Arts Sci. 8: 259, 1870; "Gilia linearis var. subulata" Gray Syn. Fl. N. A. (ed. 2) 1(2) & 2(1) Suppl.: 135: 1886; "Gilia elmeri" Piper ex Brand loc. cit. Differing from the typical form only in habit, this is here made: *C. tinctoria* **f. subulata** (Gray) Wherry, stat. nov. A branched growth-form.

tinctoria var. subulata subvar. luxuriosa Brand in Fedde Rep. Spec. nov. 17: 317, 1921. Preferably classified as *C. tinctoria* **f. luxuriosa** (Brand) Wherry, stat. nov. Differing in being branched and in having the corolla 15 mm. long.

unidentata Bertero ex Brand Pol.: 50, 1907; "Phlox unidentata" Bertero Merc. Chil. 16: 743 ex Colla Mem. Accad. Torino 38: 126, pl. 39, 1835. Compared with *C. grandiflora*, but actually a variant of a South American species, so made *C. cavanillesii* **f. unidentata** (Bert.) Wherry, stat. nov. Differing from the typical form in that many of the leaves bear a single subterminal tooth.[1]

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1 Under the alternative plan "C. linearis" (Cav.) Nutt. **formae soehrensi** (Phil.) Wherry, **stenosiphon** (Kunze) W., and **unidentata** (Bert.) W., stat. nov.

COLLOMIA: KEY TO SPECIES AND SUBSPECIES

DURATION perennial, with slender rootstocks; corolla somewhat funnelform; seeds unchanged or sparsely spirilliferous when wet........§ COLLOMIASTRUM

HABIT erect; leaves taper-petioled, elliptic-oblong, toothed above the middle; stamens about equalling the corolla.

STEMS 30 to 60 cm. high; leaves to 8 cm. long; corolla orange to salmon, about 30 mm. long, the lobes acute; endemic in e-centr. Calif. ....C. *rawsoniana*

STEMS 15 to 30 cm. high; leaves to 6 cm. long; corolla violet, about 20 mm. long, the lobes obtuse; endemic in s. Ore.................C. *mazama*

HABIT depressed; leaves mostly less than 4 cm. long; corolla violet to lavender, pink, or white, 10 to 35 mm. long, the lobes obtuse.

LEAF-CUTTING of a pedate type, often so deep that the blade is compound; calyx 6 mm. long; corolla pale, 12 to 15 mm. long; stamens equalling the corolla; nw. Wash. to ne. Calif.................C. *larseni*

LEAF-CUTTNG of a pinnate type, never so deep as to make the blade compound; calyx (6) 8 to 10 mm. long; c. Wash. to w. Mont. & n. Utah..C. *debilis;* ssp.:

STAMENS exserted; leaves from deeply 5-lobed to entire.

COROLLA lavender, 15 to 20 (25) mm. long..............................*typica*

COROLLA bright pink, (20) 25 to 35 mm. long......................*ipomoea*

STAMENS included; leaves from deeply trifid to entire....................*trifida*

DURATION annual; corolla funnelform to salverform; seeds more or less spirilliferous and mucilaginous when wet.

LEAF-OUTLINE oblong, elliptic, or spatulate, taper-petioled, the lower ones deeply pinnatifid to incised; locules pluriovulate..........§ COURTOISIA

LEAF-CUTTING usually marked; mature calyx 7 to 8 mm. long; s. B. C. to n. Ida. and s-centr. Calif...C. *heterophylla*

LEAF-CUTTING slight; mature calyx 10 to 12 mm. long; endemic in n. Calif..C. *diversifolia*

LEAF-OUTLINE linear-elliptic to broadly lanceolate, entire or coarsely few-toothed toward the tip; locules mostly uniovulate........§ EUCOLLOMIA

INFLORESCENCES compact compound cymes.

BRACTS herbaceous; corolla red, 8 to 20 mm. long; Bolivia to Patagonia, S. A...C. *cavanillesii* ("linearis")

BRACTS scarious basally; corolla never red; N. A.

COROLLA-LENGTH 15 to 30 mm., the tube much exceeding the calyx; hue salmon to cream; B. C. to w. Mont. s. to Calif. & w. Colo..C. *grandiflora*

COROLLA-LENGTH 10 to 15 mm., the tube little exceeding the calyx; hue pink to whitish; w.-temp. N.A. to Great Lakes & N. B.; adventive further se.......................C. *linearis* ("parviflora")

INFLORESCENCES open cymes, paired or solitary flowers.

COROLLA-HUE violet; length 4 times calyx; Chile, S.A.............C. *biflora*

COROLLA-HUE yellow, purplish, or whitish; N.A.

MATURE CALYX 8 to 9 mm. long; corolla little longer; sepals 1/3 united, the free part aristate; n. Ore.......................*C. macrocalyx*

MATURE CALYX 4 to 8 mm. long; corolla much longer.

SEPALS 1/2 united, the free part subulate-aristate, the junction-plications subcallous-margined; Wash. to w. Mont., s. to c. Calif. & Nev...*C. tinctoria*

SEPALS 2/3 united, the free part deltoid, acute, the junction-plications callous margined with a papilla below each sinus; Wash. to w. Wyo., s. to Utah; Calif.? ....*C. tenella*

The species-sequence followed in the above more or less natural key is based on the view that the probable course of evolution in the genus has been: perennial to annual duration; large to small size; lobed to entire leaves; and complex to simple inflorescences. In general, evolution seems to have been divergent rather than linear, thus:

—maz. —lar. —het. —gra. —mac. —ten.
/ / / / / /
ancestor..
\ \ \ \ \ \ \
—raw. —deb. —div. —cav. —lin. —tin. —bif.

For filing species in systematic order, the following plan may be used:

COLLOMIA: SYSTEMATIC GROUPING OF SPECIES

§ COLLOMIASTRUM
1. *mazama*
2. *rawsoniana*
3. *larseni*
4. *debilis*

§ COURTOISIA
5. *heterophylla*
6. *diversifolia*

§ EUCOLLOMIA
7. *cavanillesii* ("linearis")
8. *grandiflora*
9. *linearis* ("parviflora")
10. *macrocalyx*
11. *tinctoria*
12. *tenella*
13. *biflora*

To bring out the geographic relations, the species may also be arranged with reference to the approximate positions of the dispersal-centers of each; the more restricted endemics are here marked by a *.

Pacific border	Cascades-Sierras	Great Basin	Rocky Mountains	Eastern N. A.
....	....	*linearis*..........	....	....
....	*grandiflora*..........	....		
heterophylla..........	....	....		
	larseni		*debilis*	
	*mazama**	*macrocalyx**		
*diversifolia**	*tinctoria*	*tenella*		
	*rawsoniana**			
*biflora**				
cavanillesii				

The relation of evolution to geography in the genus *Collomia* now merits discussion. The ancestor of the group is inferred to have grown in western Canada so far south that none of its descendants reached Eurasia in the course of their natural migration, — the *C. grandiflora* growing in Europe having been introduced by man. During the Tertiary, evolution led to the development of the three trends represented in the sections, and one or more members of each of these migrated southward along the Cascade and Rocky mountain ranges far enough to escape glaciation.

In the course of the Pleistocene, with its alternating moist and dry stages, further evolution and migration occurred. Noteworthy are: the reduction of the two presumably most primitive members of § *Collomiastrum* to restricted endemics; the evolution of § *Eucollomia* into numerous entities; and the fact that two members of the latter section succeeded in following the same mysterious route from Mexico to middle South America as two other genera of the family, — *Microsteris* and *Polemoniella*.

No "age-and-area" correlation can be recognized, the wide-ranging species being merely those most adaptable to variations in environment.

Gymnosteris

A second refugee from *Gilia* is a group of tiny annuals characterized by persistent connate cotyledons, a leafless stem, and a capitate-cymose inflorescence subtended by connate lanceolate-ovate entire scarious bracts. Originally christened a *Collomia* by Hooker and Arnott,[1] the group was shifted to *Gilia* by Gray[2] and to *Navarretia* by Kuntze.[3] That it deserves generic independence was urged by Greene[4] who coined for it the descriptive epithet *Gymnosteris*. Finally, it was assigned to the genus *Linanthus* by Howell.[5] It has the distinction of never having been placed in the genus *Phlox;* and Kuntze failed to get around to making it a *Polemonium*.

The calyx of this group showing no trace of a differentiated junction-membrane in its calyx, the writer is unable to associate *Gymnosteris* with the Gilioid subdivision of the *Polemoniaceae;* it belongs, with *Navarretia,* to the Collomioid subdivision. All the annual Collomias tend to have persistent cotyledons, and the original dwarf form of *C. tinctoria* has an essentially leafless stem. The bracts of *C. grandiflora* would have to undergo but little evolutionary change to yield those of a *Gymnosteris;* and if the calyx-plications of any *Collomia* should contract, the Gymnosteroid calyx would result. There is no reason to believe that the present genus originated from any single existent species of *Collomia,* but the ancestor of the two genera may well have been the same.

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1 Bot. Beechey's Voy.: 368, 1841.

2 Proc. Amer. Acad. Arts Sci. **8**:266, 1870.

3 Rev. Gen Pl. **1/2**:433, 1891.

4 Pittonia 3:303, 1898.

5 Flora N.W. Amer. **1**, fasc. **4**:456, 1901.

NAMES PROPOSED UNDER THE GENUS GYMNOSTERIS

leibergii Brand in Fedde Rep. Sp. nov. 17: 318, 1921; "Gilia involucrata" Coville & Leiberg ex Brand. Differing but slightly from a previously named entity, this is here made: *Gymnosteris parvula* **f. leibergii (Brand)** Wherry, stat. nov. A variant with especially small flowers.

minuscula Jepson Man. Flg. Plts. Calif.: 809, 1925. Accepted as species.

nudicaulis (Hooker & Arnott) Greene Pittonia 3: 304, 1898, as to epithet though not entity; "G. pulchella" Greene as to entity; "Collomia nudicaulis" Hooker & Arnott Bot. Beechey's Voy.: 368, 1841; "Gilia nudicaulis" Gray Proc. Amer. Acad. Arts Sci. 8: 266, 1870; "Navarretia nudicaulis" Kuntze Rev. Gen. Pl. 1/2: 433, 1891; "Linanthus nudicaulis" Howell Fl. NW. Amer. 1, fasc. 4: 456, 1901. Regarded as the type species of the genus, in spite of Greene's confusion.

nudicaulis var. parvula Jepson loc. cit. Kept as a species here.

nudicaulis var. pulchella (Greene) Brand Pol.: 151, 1907; "G. pulchella" Greene Pittonia 3: 304, 1898. Greene had somehow got the idea that the original "Collomia nudicaulis" was the entity with relatively small calyx and corolla, so proposed an independent epithet for the large-flowered one. Actually the Hooker-Arnott plant, as shown by a good cotype in the Gray Herbarium, has moderately large flowers. A status change is accordingly called for: *G. nudicaulis* **f. pulchella** (Greene) Wherry, stat. nov. A variant with the corolla up to 15 mm. long.

parvula (Rydberg) Heller Muhlenbergia 1: 3, 1904; "Gilia parvula" Rydberg Mem. N. Y. Bot. Gard. 1: 320, 1900, not *G. parvula* Greene Pittonia 1: 72, 1887; "Gymnosteris nudicaulis" sensu Greene Pittonia 3: 304, 1898, not "Collomia nudicaulis" Hooker & Arnott loc. cit.; "G. nudicaulis var. parvula" Jepson Man. Flg. Plts. Calif.: 809, 1925. A species.

rydbergii Tidestrom Contr. U. S. Nat. Herb. 25: 437, 1925. A substitute for *parvula* of Rydberg because of this epithet being a homonym under *Gilia*.

GYMNOSTERIS: KEY TO SPECIES

HEIGHT over 1 cm.; range wide, at moderate elevations.

STEM up to 15 cm. high; sepals about 5 mm. long; corolla-tube 10 mm. long, much exceeding the calyx; limb 10 mm. across; stamens and styles subexserted; Ore., Ida. & Nev. .... *G. nudicaulis*

STEM up to 8 cm. high; sepals about 4 mm. long; corolla-tube 5 mm. long, little exceeding the calyx; limb 5 mm. across; stamens and styles included; Ore., Wyo., ec. Calif. & c. Colo. .... *G. parvula*

HEIGHT under 1 cm.; endemic above 10,000 ft. in s. Calif. .... *G. minuscula*

Size-Frequency Characteristics of Abies Fraseri Pollen as Influenced by Different Methods of Preparation[1]

Stanley A. Cain

No study of the pollen grains of the southern balsam fir, *Abies Fraseri* (Pursh) Poir., from the highest mountains of Virginia, North Carolina, and Tennessee, has been published which would assist in the identification of the species in investigations of southern sediments. In some studies, for the Soil Conservation service, of buried soils of the Piedmont in the vicinity of Spartanburg, South Carolina, numerous grains of Abies were encountered along with Picea and, probably, *Pinus Banksiana*,[2] indicating the possibility of a consideably different climate during the time of deposition than now prevails in the region. It has been assumed in that unpublished work that the fir found in the buried soils was probably *Abies Fraseri* which today occurs natively at a distance of about 100 miles and with a lower altitudinal limit of some 3000-4000 feet higher than Spartanburg.

The present study was designed to provide an adequate size-frequency characterization of *Abies Fraseri* to assist in its identification and, also, to present an analysis of any effect on size characteristics that might be due to the technique of preparation of pollen grains for study.

Fresh pollen of *Abies Fraseri* was collected on June 7, 1943, from trees along the North Carolina-Tennessee state line at an elevation of around 6000-6500 feet near the southern limits of distribution of the species on Clingmans Dome. These collections were air-dried in the laboratory, and pollen grains were prepared for microscopic study by four methods. In each case some of the dried strobili were crushed and rubbed against a brass sieve with 0.5 mm. holes. The material passing through the sieve was collected directly in centrifuge tubes by means of a funnel and by washing with the chemicals of the particular method.

In the acetolysis method the pollen-bearing materials were brought to a boil in a mixture of nine parts of acetic anhydride and one part of concentrated H_2SO_4. After centrifuging and decanting, the precipitate was twice washed in water, stained by safranin, and transferred to 95 per cent C_2H_5OH for two washings. After the final centrifuging the alcohol was decanted except for about 0.5 cc. The remainder was stirred in with the pollen material and subsequently spread upon slides, allowed to dry enough to stick the grains, and mounted in Sirtillac[3] under 24 x 10 mm. covers. In the KOH method

[1] Contributions from the Botanical Laboratory, The University of Tennessee, N. Ser. No. 66.

[2] Stanley A. Cain, *Amer. Jour. Bot.* **27**:301, 1940.

[3] The Microtechnique Shop, Indianapolis, Indiana.

material similar to the above was heated in 10 per cent KOH for about 20 minutes, but not boiled. It was then washed, stained, transferred to alcohol, and mounted as in the acetolysis method. In the alcohol method, similar material was warmed in 95 per cent C_2H_5OH for about five minutes and subsequently treated as above. For the sake of a standard with which to compare the above techniques, similar pollen-bearing material was boiled about five minutes in distilled water, stained, and mounted in five per cent glycerin.

A random sample of 100 grains was measured for each of the four types of preparation. A compound binocular was employed for the measurements. It was equipped with 10x oculars and an 8 mm. objective (20x), and an ocular micrometer in which one line equals 2.83 microns. In each case a transverse measurement was made on the body of the grain between the dorsal roots of the bladders, with the cap excluded. This measurement could be made from grains seen in transverse optical section: laterally, dorsally (bladders down), and ventrally (bladders up, furrow showing). As strips across a slide were observed by use of a mechanical stage, every expanded and undistorted grain lying in a suitable position was measured, and thus a random sample was obtained.

TABLE 1.—Size-Frequency Characteristics of *Abies Fraseri* Pollen Prepared by Different Methods.

Method of preparation	Size of grains in microns 96.2	92.9	90.6	87.7	84.9	82.1	79.2	76.4	73.6	70.7	67.9	65.1	62.2
Acetolysis	..	1	6	8	8	14	22	25	11	4	1	..	..
Alcohol	..	..	1	1	2	4	9	18	25	20	10	8	2
KOH	1	4	5	10	10	16	19	14	10	5	4	2	..
Water	..	..	..	..	4	6	15	17	21	20	10	6	1

The size-frequency distributions for *Abies Fraseri* pollen grains prepared by the methods described are presented in Table 1. It is obvious that there is a considerable range of grain sizes, and that modes are evident but not strongly developed. Size distributions seem to be comparable for the acetolysis and KOH methods on one hand and for the alcohol and water methods on the other. It was decided to carry the analysis further, and Table 2 gives the

TABLE 2.—Statistical Characteristics of *Abies Fraseri* Pollen Grains Prepared by Different Methods.

Method of preparation	Mean[4]	Sigma $= -\sqrt{\frac{\Sigma D^2}{n}}$	Probable error of mean $= 0.6745 \frac{\text{Sigma}}{\sqrt{n}}$
Acetolysis microns	79.8	± 5.15	± 0.348
Alcohol microns	73.3	± 5.26	± 0.356
KOH microns	80.4	± 6.62	± 0.447
Water microns	74.1	± 5.07	± 0.342

4 The calculations were made on a basis of ocular lines and converted to microns as this made the calculations somewhat simpler. The calculations on which Table 3 were made are not converted to microns.

means, standard deviations, and probable errors of the means for the sets of measurements. The apparent similarity of size characteristics of the grains prepared by the acetolysis and KOH methods (79.8 and 80.4 microns, respectively), and likewise of those prepared by the alcohol and water methods (73.3 and 74.1 microns, respectively) is verified by the lack of statistical significance between their means, as shown by Table 3. The grains prepared by the acetolysis and KOH methods, however, average considerably larger than those prepared by the less drastic alcohol and water methods. As shown by Table 3, these differences are of a sufficient order to be statistically significant, with values (difference divided by probable error of difference) from 11.0 to 13.0 and only one chance in several thousand that the differences are a result of sampling.

It can be concluded, then, that pollen grains of *Abies Fraseri* prepared by acetolysis range from 67.9 to 93.4, with an average of 79.8 microns breadth — wings and cap excluded. When prepared by the KOH method, the range is from 65.1 to 95.2, with an average of 80.4 microns. By the alcohol method the range is from 62.3 to 89.6, with an average of 73.3 microns. The water method yielded a size range from 62.3 to 84.9, with an average of 74.1 microns.

It would seem that the least drastic method of preparing fresh grains by briefly boiling them in water yields results that more nearly approximate the size characteristics of untreated grains. The alcohol method produces no appreciable difference from the water method, and the acetolysis and KOH methods result in an average grain size of about 8.5 per cent larger. I do not mean by these remarks to recommend the exclusive use of the alcohol method in the preparation of peats and other sediments for pollen analysis. Strongly

TABLE 3.—Statistical Comparisons of Means of *Abies Fraseri* Pollen Prepared by Different Methods.

Preparations compared	Difference in lines	Probable error of differences	$\frac{D}{\sqrt{p.e.m^2 + p.e.M^2}}$
Acetolysis vs. C_2H_5OH	2.3	0.176	13.0
Acetolysis vs. KOH	0.2	0.200	1.0
Acetolysis vs. H_20	2.0	0.172	11.6
C_2H_5OH vs. KOH	2.5	0.202	12.3
C_2H_5OH vs. H_2O	0.3	0.175	1.7
KOH vs. H_2O	2.2	0.199	11.0

consolidated peats do not yield to this treatment, especially after drying, and quantities of cellulose and lignified materials frequently clutter up the preparations. Of the stronger chemicals, it has been my experience that the acetolysis method results in better preparations for diagnostic purposes and less damage to grains than does the KOH method. At any rate, it is useful to have an indication of the effects of the various methods as the acetolysis technique is widely used by European workers and the alcohol and KOH methods by most American investigators.

One collection of *Abies balsamea* (L.) Mill. pollen was available to me, obtained from the New York Botanical Garden in 1939. Measurements of 100 grains of this species from material prepared by acetolysis showed it to have a size range (65.1 to 90.6 microns) and a mean (78.2 microns) entirely comparable to *Abies Fraseri*. The size-frequency technique, if these are representative samples, offers no aid to identification of these species by pollen grains.

An interesting result of this study is the indication that the fossil Abies of the buried soils near Spartanburg, mentioned in the introductory paragraph, does not correspond in size to either *Abies Fraseri*, which today is closest, or to *Abies balsamea*, which extends from northeastern United States as far down the Appalachians as Virginia. Table 4 shows that the fossil material is composed of grains as large as any among the American representatives of the genus, insofar as the meagerly published information admits comparison. They range from 88.9 to 110.7 microns with a mean of 101.1 microns, and are about 27 per cent larger, on the average, than *Abies Fraseri*, and 29 per cent larger than *Abies balsamea*.

The only other native fir in the eastern United States is *Abies intermedia* Fulling, a possible hybrid between *Abies Fraseri* and *Abies balsamea*, with a restricted distribution in the Shenandoah area of the Virginia Blue Ridge where the ranges of the species approach each other. The size characteristics of the pollen grains of *Abies intermedia* are not known (no pollen seems to be available at present), but it is unlikely that they are as large as the fossil ones under question.

TABLE 4.—Size Characteristics of Abies Pollen Grains Exclusive of Bladders.

Species	Range in microns	Mean in microns	Author
Eastern Species			
Fraseri[5]	67.9 — 93.4	79.8	Cain
balsamea[5]	65.1 — 90.6	78.2	Cain
balsamea	50.0 — 104.0	±90.0	Wodehouse[6]
Western Species			
venusta	83.0 — 88.0		Wodehouse
lasiocarpa[7]	78.0 — 91.0	±90.0	Wodehouse
grandis[7]	78.0 — 91.0	±90.0	Wodehouse
amabilis[7]			Hansen
concolor[7]	85.5 — 97.0		Wodehouse
nobilis[7]	96.0 — 109.0		Wodehouse
magnifica	90.0 — 104.0	± 100.0	Wodehouse
Piedmont Fossil			
species?[8]	88.9 — 110.7	101.1	Cain

5 Fresh material prepared by acetolysis; measurements based on 100 grains.

6 Measurements from R. P. Wodehouse (Pollen Grains, pp. 263-266. 1935); means are approximate and number of measurements not stated.

7 Size sequence according to H. P. Hansen (Northwest Sci.: 14, 9 pp., 1940, and Amer. Midl. Nat. **27**:523-534. 1942); no measurements given in the publications.

8 Measurements based on 29 grains from profile IV, Spartanburg, South Carolina, buried soils, which were undistorted and lay in a position for accurate measurement; acetolysis preparation.

I do not believe that the large size of the fossil grains, and their comparability in that respect to certain western species (Table 4), indicate that *Abies nobilis* or *Abies magnifica* once lived in the eastern Piedmont. It is just as likely that the fossil grains represent an extinct species (or an anomaly for some unsuspected reason) — for no one knows, even approximately, the age of the Spartanburg buried soils.

Summary

Fresh, mature pollen grains of the southern balsam fir (*Abies Fraseri*) were prepared by four methods for size-frequency analysis. Treatment with 95 per cent alcohol did not significantly change the grains from the size found in comparable materials merely boiled in water. The widely used acetolysis and KOH methods of preparation of peats for pollen analysis and of "fossilization" of fresh grains, however, result in an apparent grain swelling of 8.5 per cent, which is shown to be statistically significant.

Certain fossil Abies pollen grains from buried soils in the South Carolina Piedmont were shown to have size characteristics over one-fourth larger, on the average, than the eastern species of fir, *Abies Fraseri* and *Abies balsamea*. The identity of the fossil fir remains unknown.

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Notes on the Ecology of the Fungi of Mount Shasta

Wm. Bridge Cooke

1. Biological Factors

Morphological aspects.—In the vegetative condition, most fungi, consisting as they do of a mycelium which penetrates the substratum as a network of more or less anastomosing, hyaline or colored threads, look much alike. The hyphae may be coenocytic or composed of long or short cells, may bear specialized structures such as clamp connections, may produce oidia or chlamydospores and may be organized into rhizomorphs. But whether the mycelium be located in living host tissues, in rotting organic remains or on decomposed matter on the surface or in the soil, the special characteristics which may be noted permit identification, for the most part, only so far as the major group to which any species belongs. Only in the fruiting condition can differences between less than major groups be distinguished. A number of ecological adaptations have been evolved in the fructifications of the higher fungi, the Ascomycetes and Basidiomycetes. In the Ascomycetes, the Pyrenomycetes produce perithecia or hysterothecia which are imbedded either in a stroma or in host tissues and which are rarely truly superficial; in the larger number of species they are carbonaceous and thus possibly protected from drought. Most of the operculate Discomycetes produce fleshy apothecia which are soon putrescent. In most of the inoperculate Discomycetes the apothecia are more or less leathery; the ability of such apothecia to fold up during brief periods of unfavorable conditions is a response to drought which may also be a protection to the fructification. In the Basidiomycetes, three modifications of the fructifications appear to be ecologic. In the Tremellales, the basidiocarps are usually highly gelatinous. One which has not shed all its spores may dry up, without disintegrating, at the end of a favorable period, resuming activity again when sufficient moisture is present. The boletes and most of the agarics are fleshy, the basidiocarps purtrefying rapidly within a few days after their emergence. In the other groups, the fructifications usually have a leathery or woody consistency and are sometimes perennial. In these groups, spores may be produced over long periods, the intervals of active spore production separated by times of short to prolonged drought (cf. A. H. Reginald Buller, Researches on Fungi, Vol. 1, 1909).

The classification of the life forms of the fungi must be based on either the vegetative or fruiting condition. Because of the nature of the vegetative condition, emphasis must of necessity be on the latter.

Physiological aspects.—The adjustment of a heterotrophic organism to its source of food has long been discussed. Whether fungi began as pathogens and some became saprogens or the reverse has never been decided. Certainly,

at the present time some are pathogens, some saprogens, and some so weakly pathogenic that it is difficult to classify them in either category. Another problem which has long been of interest is the adjustment of a number of species of fungi to a single host or substratum. The succession of species of fungi on dung has often been noted, as has the succession on logs. The death of a tree may be caused by the weakening effect of one or more heart or butt rots. After falling, the log may be invaded by additional heartwood rots, by the penetration of sapwood rots and finally by a number of other fungi whose activities may be wide-spread or localized. Certainly, there is some relationship between these various fungi, either of antagonism, of communism or of indifference.

All fungi require water both for vegetative growth and for rapid elaboration of fructifications, except those of carbonaceous or woody texture. Thus, the appearance of the fructification may be a measure of the precipitation of a region at a particular time. It follows that the mycobiota of a given region need not be identical in two successive seasons, either in the case of saprogens or pathogens. There are no data available as to the percentage of annual as contrasted with perennial fungi. Certainly, some wood rots live for many years, as evidenced by the fructifications or by the extent of the invasion of standing timber. Again, many soil or humus fungi fruit only at long intervals (apparently in coordination with climatic cycles), which indicates the perennial character of the mycelium. On the other hand, in the case of certain leaf spots the perfect stage is found in the spring on the fallen host leaves. Since there is no evidence of a perennial mycelium within the twigs and branches of the host, these may be considered annual fungi. In regions where the ground is covered with snow during long periods of the year, certain fungi inhabiting dead remains of the previous year's vascular flora produce mature perfect fructifications by the following spring. This is also true of related fungi in regions where the snow is replaced by rain, but it is most striking in the snow country.

Methods of spore dispersal.—The spores of most of the fungi found on Mt. Shasta are wind-borne, but some are dispersed by other means. The spores of some, perhaps all, of the hypogaeous fungi are dispersed by rodents. When fresh, these fungi emit an odor which is usually noticeable before they are dug out of the duff or humus in which they are imbedded, although to human senses it may be merely what is referred to as a "fungus" odor. Representatives of several hypogaeous species have been found lying on stumps and logs, apparently left to dry for winter storage after some rodent had taken a few nibbles out of them. *Secotium nubigenum* is commonly found partly eaten or left whole on tops of logs drying in the sun. Specimens of an undetermined species of *Russula* have been found in similar positions. *Boletus albidus* ssp. *eupachypus* in its ordinary habitat under the top layer of duff is rarely in perfect condition because tooth marks of rodents indicate parts of the sporophore have been eaten away. In other cases it is evident that deer also eat this species of *Boletus,* for no rodent on the mountain is large enough to eat entire caps or dig large holes to reach them. In collecting this species it is

usually a race between the collector and its mammalian mycophagists. It has not been demonstrated that passage through the mammalian alimentary canal is necessary for the germination of these spores. In some cases beetles possibly assist in the dissemination of fungus spores, as in the case of the bark fungus, *Cryptoporus volvatus*.

2. Ecological Factors

Lack of correlation with life zones.—The life zone concept of Merriam was based largely on the temperature requirements of vascular plants and zones were delimited on the basis of fairly constant plant associations found in certain broad latitudinal and comparable altitudinal regions. It is demonstrable that fungi do not follow these zonal areas with as great regularity as do the vascular plants, at least in temperate and arctic or alpine areas. Diehl has noted the restriction of most Xylariaceae and Phallales to the tropics, and no representative of these groups has so far been found above 4000 feet on Mt. Shasta. However, many of our fungi are not restricted by elevation or life zones, as is demonstrated by the accompanying list.

Snowline fungi.—One of the most interesting phases of the problem of the ecology of Mt. Shasta fungi is that of saprobic species growing in duff and on logs close to melting snow banks. Except for such melting as may take place on their under sides during the winter, the melting of these snow banks during the warm weather of early summer provides the only moisture available to these fungi. The infrequent summer rains evaporate or percolate so rapidly that they can do no more than revive dry sporophores. The only reservoir of moisture which fungi can utilize, therefore, is that provided by melting snow banks. This reservoir is available for several weeks after melting since, if much snow has fallen, percolation takes a long time and duff and logs hold the moisture longer than open soil and the top layers of newly fallen leaves.

Where a large quantity of duff has accumulated and is augmented by chips, rotting stumps and similar debris, several saprogenic fungi occur. At the time the snow banks are melting away from such a place, it is possible to study the areas of activity of the saprogens as represented by their sporophores. Within a few feet of the snow bank *Pseudoplectania fulgens* and *Paxina nigrella* are receiving enough moisture from their mycelia to be turgid and apparently active. But even within ten feet of the snow bank the sporophores, although with quantities of undischarged spores, are dry and shrunken and difficult to find. At intervals of about four days one such location was visited several times in late June and early July, 1941. Here it was found that as the snow bank retreated the area of sporophore activity advanced, so that over twenty sporophores were collected on each of three visits, each of the colonies being in a different location and each about the same distance from the snow bank.

In the case of larger sporophores, such as those of the subfleshy *Secotium nubigenum*, a somewhat similar condition was observed. Although occasional specimens were found elsewhere, the best collecting occurred on rotting logs

in the vicinity of snow banks. Another factor favoring the greater abundance of these fructifications in such places is that squirrels do not usually cross snow banks in order to get their food. Whenever possible, rodents — golden-mantled squirrels mostly, and probably also the Tahoe chipmunk and the Douglas tree squirrel — dry them and store them for food. *Mycena griseo-virida* is another fungus whose fructifications are found close to melting snow banks or even growing up through thin patches of snow. This species fruits only where logs and rotting wood are kept wet by the run-off from the snow banks. As soon as the substratum dries, the sporophores also dry.

On rotting logs near snow banks the fructifications of two polypores occur. These may become activated by occasional rare rains but only for short periods of time. *Polyporus (Aurantioporellus) alboluteus* is nearly resupinate, bright orange-red and occurs on the under side of logs. It is rarely found in good condition more than a week or ten days after the snow has melted. After this time usually all that is left is a heap of red dust and a few inedible fragments left by the small beetles which feed on it by hundreds. *Polyporus (Spongiporus) leucospongia* is rarely attacked by beetles and its dried sporophores are found throughout the summer on the higher parts of the mountain wherever wood occurs. It is fresh only when watered by melting snow, although occasional light summer rains appear to revive it. Other fungi may be producing active sporophores on the same log during the dry season, and the mycelium of this species may be active, but the sporophores remain dried out.

Another series of fungi, common to coniferous hosts throughout a wide range, is found on the rotting wood of Shasta fir in the upper portions of its altitudinal range on Mt. Shasta. Among these are: *Coniophora olivacea, Corticium roseum, Dacrymyces deliquescens, Oxydontia alboviride, Pellicularia flavescens, Cristella candidissima, Poria lenis, Solenia candida* and *Tremellodon gelatinosus*. Of course, some of these species are not confined to coniferous wood, or even to wood. They are not confined to any altitudinal limits, occurring as commonly at sea level as at 8000 feet.

Still another series of fungi is confined, more or less, to higher elevations and is usually found in association with melting snow banks. Probably there is a close relationship between the physiological requirements of these fungi and the conditions found in the immediate proximity of melting snow. These fungi include: *Stereum rugisporum, Mycena griseoviride, Polyporus alboluteus, Polyporus leucospongia, Secotium nubigenum, Pseudoplectania fulgens, Paxina nigrella* and others. The range of these fungi, so far as known, is mostly in the higher elevations of the Sierra Nevada, Cascade and Rocky Mountain ranges.

Host restriction.—A number of species in the Mt. Shasta mycobiota are restricted to certain hosts. This restriction is either artificial or real. If it is artificial, we have as yet no evidence, through cross inoculations, for that fact. Such inoculations can furnish the answer to the question as to whether morphologically similar species growing on different hosts and hence listed as

distinct species, are in reality the same. To the extent to which their hosts are restricted to certain life zones, these fungi are likewise restricted and in certain cases the range of the fungi is less than that of the hosts. When this occurs in the same life zone, it can possibly be explained on the basis of barriers to the distribution of the fungus. These would include up-drafts or down-drafts which would be restricted to certain valleys and the presence of ridges between the several communities of plants across which fungus spores would have no normal means of passage.

3. An Ecological Classification of Mt. Shasta Fungi

The ecological classification of fungi on the basis of the water content of the substratum or medium into xerophytes, mesophytes, hydrophytes and halophytes is of very limited application. A fungus may have concealed sources of water supply which are not easily determined except in the case of certain soil fungi growing in deserts, the water molds and the parasites of aquatic organisms. The classification of fungi on the basis of their life form has been referred to. For the present purpose, fungi may be classified on the basis of their relationship to their hosts or habitats:

1. *Saprogens*. Annual or perennial fungi which live in the soil or on dead organic remains.

2. *Weak pathogens*. Mostly annual fungi, at least so far as their living host is involved, which attack leaves of vascular plants and cause minor local infections. In most cases, the perfect stage is unknown or poorly understood.

3. *Strong pathogens*. Annual or perennial fungi which live all or part of their lives within the living or dead tissues of living plants. In the case of the leaf spots due to imperfect fungi, the perfect stage is commonly developed after the diseased part of the host has died. For instance, numbers of hyphal knots which appear to be pycnidial or perithecial initials are found in the sori of *Ramularia Senecionis* var. *carniolica*, although no spores have been observed in these structures. Possibly these mature after the short-lived host tissues have died. Heartwood and butt rots can be included here because of the eventual damage due to their action in the dead tissues of the tree trunks.

4. Geographic Relationships

Cosmopolitan species.—A number of the fungi collected on Mt. Shasta are of extremely wide distribution. Wood rots such as *Porodaedalia Pini*, humus species, such as *Polyporus (Coltricia) perennis*, molds, such as *Pleospora herbarum*, pathogens, such as *Scoletotrichum graminis* and many other species are of world-wide or continent-wide distribution wherever suitable hosts and growth conditions occur.

Western species.—Throughout the western states a number of fungi are common pathogens, weak pathogens or saprogens on wide-spread species, groups of species or whole orders of vascular plants. Among these are the

more common heartwood and sapwood rots, and a number of secondary rots and molds.

Local species.—A third group of fungi is composed of those in which the range is incompletely known. This includes cases in which the fungus is known from but a single collection or from few collections, or from a host which, so far as collections indicate, has a wider range than its pathogens. On Mt. Shasta, *Aleurodiscus fruticetorum, Boletus frustosus, Merulius atropurpureus, Oidium magnisporum, Phyllosticta Fritillariae, Phyllosticta Monardellae, Galeropsis polytrichoides, Septoria shastense* and *Ustilago shastense* are among the species not yet known elsewhere.

In connection with geographic distribution, it has commonly been noted that many fungi have strikingly discontinuous ranges. In some cases, species are fairly well known in Europe and are not to be found again except in the western United States. Two cases of such discontinuous distribution may be cited: *Hymenogaster Remyi,* known only from mountains in France and from Mt. Shasta; *Hysterangium Darkeri,* known only from the Wasatch Mountains near Salt Lake City and from Mt. Shasta. The unintentional collection of fungi by collectors of vascular plants when they include diseased leaves in their collections has done much to increase the known range of some fungi when such collections have been examined with the purpose of detecting the fungi. In the case of other fungi, neglect of areas by both plant collectors and mycologists has left large discontinuous unknown areas.

According to Bisby: "The distribution of the fungi is primarily controlled by the distribution of their hosts and substrata." The writer prefers to restate this proposition as follows: The distribution of fungi is primarily controlled by their adaptability to hosts and substrata regardless of the relationship of these latter organisms to each other and regardless of the altitudinal distribution of these host organisms.

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REFERENCES

1. BISBY, G. R. 1933—The distribution of fungi as compared with that of phanerogams. Amer. Jour. Bot. **20**:246-254.

2. COOKE, W. B. 1940-1941—Flora of Mt. Shasta. Am. Midl. Nat. **23**:497-572. 1940. First Supplement. Am. Midl. Nat. **26**:74-84.

3. ———1941—The problem of life zones on Mt. Shasta. Madroño **6**:49-56. 1941.

4. DIEHL, W. W. 1937—A basis for Mycogeography. Wash. Acad. Sci. Jour. **27**: 244-254.

LOVELAND, OHIO.

TABLE 1.—List of Mount Shasta Fungi According to Host and Altitudinal Range.

Column 1.—List of Fungi found on Mt. Shasta to September, 1942
2.—List of hosts on which these fungi are found. If no definite host is involved appropriate substratum notes are given.
3.—Elevations at which hosts are found.
4.—Elevations at which fungi are found.
5.—S—Sabrobe; P—Pathogen; W—Weak Pathogen.
6.—A—Annual; P—Perennial. Observations in this column based on longevity of parts of host on which fungus is found.

Abstoma reticulatum	hypogaeous		8000	S	P
Agaricus arvensis	humus		8000	S	P
Aleurodiscus amorphus	*Abies concolor*	4–6000	55–6000	S	P
	Abies magnifica shastensis	5–8500	6–7000	S	P
diffissus	*Arctostaphylos nevadensis*	5–9000	8000	S	P
	Arctostaphylos patula	4–8000	6000	S	P
fruticetorum	*Arctostaphylos patula*	4–8000	6000	S	P
	Ceanothus velutinus	4–8500	6000	S	P
Amanitopsis vaginata	humus		5000	S	P
Aposphaeria mollis	*Juncus parryi*	7–8500	7000	S	A
Archangeliella lactarioides	hypogaeous		8000	S	P
Armillaria mellea	*Abies magnifica shastensis*	55–8500	5–8000	P	P
	Pinus lambertiana	4–6000	5500	P	P
Ascochyta oudemannsii	*Stipa occidentalis*	4–8500	7000	W	A
Barssia oregonensis	hypogaeous		8000	S	P
Boletus albidus eupachypus	humus		7–8000	S	P
frustosus	humus		7500	S	P
miniato-olivaceus	humus		5000	S	P
Bovista pila	humus		8000	S	P
Calodon amicus	humus		7000	S	P
Calvatia sculpta	humus		6–7000	S	P
Cintractia caricis	*Carex multicaulis*	7–8000	75–8000	P	A
	Carex nigricans	75–8500	8000	P	A
	Carex spectabilis	75–8500	75–8500	P	A
externa	*Carex spectabilis*	75–8500	8000	P	A
Cladosporium herbarum	*Agrostis* sp.		8000	S	A
	Carex sp.		8000	S	A
	Juncus sp.		8000	S	A
	Phleum sp.		8000	S	A
	Trisetum sp.		8000	S	A
Clavaria obtusissima	humus		5500	S	P
pinicola	*Abies magnifica shastensis*	55–8500	8000	S	P
Clitocybe metachroa	humus		7500	S	P
Coniophora olivaceus	*Abies magnifica shastensis*	55–8500	8000	S	P
Coleosporium madiae	*Madia gracilis*	4–5500	5000	P	A
solidaginis	*Aster shastensis*	4–9000	45–5000	P	A
Coprinus comatus	humus		8250	S	P
Corticium cremoricolor	*Abies magnifica shastensis*	55–8500	8000	S	P
roseum	*Abies magnifica shastensis*	55–8500	8000	S	P
scutellare	*Abies magnifica shastensis*	55–8500	8000	S	P
Cortinarius cotaneus	humus		7500	S	P
Cristella candidissima	*Abies magnifica shastensis*	55–8500	8000	S	P
Cronartium comptoniae	*Pinus contorta murrayana*	6–7000	6000	P	P
Crucibulum vulgare	humus		8000	S	P
Cryptoporus volvatus	*Abies magnifica shastensis*	55–8500	55–8000	P	P

Cryptostictis arbuti	*Arctostaphylos nevadensis*	5–9000	4–7500	P	A
	Arctostaphylos patula	4–8000	4–5500	P	A
Cumminsella sanguinea	*Berberis piperiana*	4–5500	5000	P	A
Cylindrocolla sp.	*Abies magnifica shastensis*	55–8500	8000	S	P
Cystopus candidus	*Sisymbrium altissimum*	4–5000	4–5000	P	A
Dacrymyces deliquescens	*Abies magnifica shastensis*	55–8500	8000	S	P
Darluca filum	*Puccinia rubigo-vera*	3500	3500	P	A
	Uromyces fabae	5000	5000	P	A
Dasyscypha agassizii	*Abies magnifica shastensis*	55–8500	8000	S	P
	Tsuga mertensiana	65–8500	7800	S	P
arida	*Abies magnifica shastensis*	55–8500	8000	P	P
	Pinus albicaulis	7–10000	8000	P	P
Dendrogaster elasmomycetoides	hypogaeous		8000	S	P
Dendryphium sp.	*Poa pratensis*	4–8000	5000	S	A
Dimerium sp.	*Penstemon menziesii davidsonii*	85–9500	85–9500	P	P
Discina ancilis	humus		8000	S	P
Dothidella castanicola	*Castanopsis chrysophylla*	4–6500	4–6500	P	A
junci	*Juncus parryi*	7–8500	75–8000	S	A
Duplicaria acuminata	*Juncus parryi*	7–8500	8000	S	A
Echinodontium tinctorium	*Abies concolor*	4–6000	6000	P	P
	Abies magnifica shastensis	55–8500	6000	P	P
Elasmomyces echinosporus	hypogaeous		8000	S	P
Endogone lactiflua	hypogaeous		8000	S	P
Endogone sp.	hypogaeous		8000	S	P
Epochnium isthomorphum	*Chrysothamnus nauseosus occidentalis*	4–9000	5000	P	A
Erysiphe cichoracearum	*Cryptantha affinis*	5–5700	4–5000	P	A
	Erigeron inornatus	4–5000	4–5000	P	A
graminis	*Agrostis exarata*	5–6000	57–8000	P	A
	Poa pratensis	4–8000	5–8000	P	A
	Sitanion hystrix	5–9000	8000	P	A
polygoni	*Eriogonum marifolium*	7–9000	57–7500	P	A
	Vicia americana	5–6000	5–6000	P	A
Exobasidium vaccinii	*Arctostaphylos nevadensis*	5–9000	5000	P	A
vaccinii-uliginosii	*Arctostaphylos nevadensis*	5–9000	45–6000	P	A
	Arctostaphylos patula	4–8000	4–5500	P	A
Flammula graveolens	humus		7000	S	P
penetrans	*Abies magnifica shastensis*	55–8500	8000	S	P
Fomes annosus	*Abies magnifica shastensis*	55–8500	8000	P	P
officinalis	*Abies magnifica shastensis*	55–8500	5–8000	P	P
	Pinus lambertiana	4–6000	5500	P	P
pinicola	*Abies magnifica shastensis*	55–8500	6000	P	P
subroseus	*Abies magnifica shastensis*	55–8500	8000	P	P
Galeropsis cucullata	humus		5700	S	P
polytrichoides	humus		8000	S	P
Ganoderma oregonensis	*Abies magnifica shastensis*	55–8500	7–8000	P	P
Gautieria monticola	hypogaeous		8000	S	P
Gloeosporium pteridis	*Pteridium aquilinum pubescens*	4–6500	5700	P	A
Gloniella lapponica	*Arctostaphylos nevadensis*	5–9000	8000	S	P
Godronia sp.	*Arctostaphylos patula*	4–8000	5–6000	S	P
	Castanopsis chrysophylla	4–6500	6000	S	P
Guepiniopsis alpinus	*Abies magnifica shastensis*	55–8500	7–8000	S	P
	Pinus albicaulis	7–10000	8000	S	P
	Tsuga mertensiana	65–8500	7–8000	S	P
Gymnosporangium libocedri	*Amelanchier alnifolia*	4–6000	35–5000	P	A
	Crataegus douglasii	3500	3500	P	A
	Libocedrus decurrens	4–5000	4–5000	W	P

Helminthosporium vagans	*Poa pratensis*	4–8000	8000	W A
Helvella californica	humus		5700	S P
caroliniana	humus		5000	S P
Hendersonia distans	*Carex* sp.	8000	8000	S A
sp.	*Agrostis thurberiana*	75–8500	8350	S A
Herpotrichia nigra	*Abies magnifica shastensis*	55–8500	8–8500	W P
	Tsuga mertensiana	65–8500	8–8500	W P
Heteropatella alpina	*Aster shastensis*	4–9000	6–8500	S A
	Castilleja miniata	5–8500	8200	S A
	Pentstemon gracilentus	7–9000	8000	S A
	Juncus sp.	8000	8000	S A
	Ligusticum grayi	5–8500	8–8500	S A
Heterosporium alii	*Tritelia ixioides analina*	5–6000	5500	P A
Hyalopsora polypodii	*Cystopteris fragilis*	55–6000	5700	P A
Hydnangium parksii	hypogaeous		8000	S P
Hygrophorus gliocyclus	humus		7500	S P
russula	humus		7000	S P
vernalis	humus		8000	S P
Hymenochaete rugispora	*Abies magnifica shastensis*	55–8500	7–8000	S P
tabacinia	*Ceanothus velutinus*	4–8500	6500	S P
Hymenogaster remyi	hypogaeous		8000	S P
Hypholoma fasciculare	humus		5700	S P
Hypoderma robustum	*Abies concolor*	4–6000	5000	P A
Hypomyces aurantius	*Ganoderma oregonense*	7–8000	8000	P A
Hysterangium darkeri	hypogaeous		8000	S P
phillipsii	hypogaeous		8000	S P
separabile	hypogaeous		8000	S P
Hysterium acuminatum alpinum	*Abies magnifica shastensis*	55–8500	8000	S P
	Tsuga mertensiana	65–8500	7800	S P
magnosporum	*Athyrium americanum*	75–8500	8000	S P
Hysterographium formosum	*Abies magnifica shastensis*	55–8500	8000	S P
	Pinus albicaulis	7–10000	8000	S P
Lachnellula chrysophthalma	*Abies magnifica shastensis*	55–8500	8000	S P
Lasiosphaeria vermicularis	*Abies magnifica shastensis*	55–8500	8000	S P
Lentinus lepideus	*Pinus albicaulis*	7–10000	8200	S P
	Pinus ponderosa	4–7000	4–5000	P P
Lenzites sepiaria	*Abies magnifica shastensis*	55–8500	7000	S P
Leptosphaeria caricinella	*Juncus balticus montanus*	5–8000	8000	S A
culmorum	*Juncus orthophyllus*	75–8250	8000	S A
doliolum	*Arnica viscosa*	8–8500	8250	S A
junciseda	*Juncus balticus montanus*	5–8000	8000	S A
	Juncus orthophyllus	75–8250	8000	S A
michotii	*Juncus orthophyllus*	75–8250	8000	S A
microscopica	*Agrostis thurberiana*	8–8250	8000	S A
	Trisetum spicatum	8–8500	8–8500	S A
vagans	*Agrostis* sp., *Carex* sp.	8000	8000	S A
	Phleum alpinum	8–8500	8000	S A
	Trisetum spicatum	8–8500	8–8500	S A
sp.	*Juncus balticus montanus*	5–8000	8000	S A
	Lupinus obtusilobus	7–8500	8000	S A
Lophium sp.	*Juncus balticus montanus*	5–8000	8000	S A
Lophodermium nitens	*Pinus albicaulis*	7–10000	8000	W A
phloxii	*Phlox douglasii*	5–9000	8000	P A
Lophodermina juniperina	*Juniperus communis montanus*	82–9500	8200	W A
Macowanites magnus	hypogaeous		8000	S P
Macrophoma cylindrospora	*Phlox douglasii*	5–9000	8000	P A
Macrosporium puccinioides	*Lathyrus lanszwertii aridus*	4–6000	5000	P A
Marssonia potentillae	*Potentilla glandulosa nevadensis*	4–6000	5–6000	P A

Melampsora arctica	*Salix sitchensis*	5500	5500	P A
lini	*Linum micranthum*	4–5000	4000	P A
ribesii-purpureae	*Salix scouleriana*	4–6500	4–5500	P A
Melampsorella cerastii	*Stellaria longipes*	5000	5000	P A
Melanogaster variegatus	hypogaeous		8000	S P
Merulius atropurpureus	*Abies magnifica shastensis*	55–8500	7000	S P
bellus	*Abies magnifica shastensis*	55–8500	8000	S P
ceracellus	*Abies magnifica shastensis*	55–8500	8000	S P
Metasphaeria sepalorum	*Juncus parryi*	7–8500	8000	S A
Montagnea arenarius	humus		4000	S P
Morchella esculenta	humus		5000	S P
Mycena griseovirida	*Abies magnifica shastensis*	55–8500	8000	S P
Mycosphaerella agrostidis	*Agrostis* sp.	8000	8000	S A
aquilegiae	*Lupinus obtusilobus*	7–8500	8000	S A
Mycosphaerella tulasnei	*Juncus balticus montanus*	5–8000	8000	S A
	Phleum alpinum	8–8500	8000	S A
	Trisetum spicatum	8–8500	8250	S A
Naemosphaera shastensis	*Streptanthus orbicularis*	8–8250	8000	S A
Neopeckia coulteri	*Pinus albicaulis*	7–10000	8–9000	P A
Nyssopsora echinata	*Ligusticum grayi*	5–8500	8–8500	P A
Odontotrema minus	*Abies magnifica shastensis*	55–8500	8000	S P
Oidium magnisporum	*Abies magnifica shastensis*	55–8500	8000	S P
Ollula pezizoides	*Abies magnifica shastensis*	55–8500	8000	S A?
Oxydontia alboviride	*Abies magnifica shastensis*	55–8500	8000	S P
Paxillus panuoides	*Abies magnifica shastensis*	55–8500	8000	S P
Patella scutellata	*Abies magnifica shastensis*	55–8500	5–6000	S P
	Libocedrus decurrens	4–5000	5000	S P
Paxina nigrella	humus		7–8000	S P
Pellicularia flavescens	*Abies magnifica shastensis*	55–8500	8000	S P
Phlebia merismoides	*Abies magnifica shastensis*	55–8500	7–8000	S P
Pholiota trachyspora	humus		7000	S P
Phoma harknessii	*Pinus albicaulis*	7–10000	8000	S A
herbarum	*Castilleja arachnoidea*	7–8500	8000	S A
Phragmidium ivesiae	*Potentilla gracilis nuttallii*	4–5000	4–5000	P A
occidentale	*Rubus occidentalis*	4–5000	4–4500	P A
rosae-californicae	*Rosa gymnocarpa*	5–9000	7500	P A
Phyllosticta amicta	*Arctostaphylos nevadensis*	5500	5500	S A
caricis	*Carex bolanderi*	4–8000	7500	P A
ferax	*Lupinus albicaulis shastensis*	5–9000	5700	P A
fritillariae	*Fritillaria atropurpurea*	4–8500	6000	P A
monardellae	*Monardella odoratissima*	55–8500	6000	P A
nigrescens	*Viola purpurea*	4–8500	8000	S A
Placosphaeria shastensis	*Monardella odoratissima*	4–8000	7500	S A
Pleospora amplispora	*Lupinus albicaulis shastensis*	8–8500	8250	S A
anthyllidis	*Arnica viscosa*	4–8000	7–8000	S A
balsamorhizae	*Lupinus albicaulis shastensis*	7–8500	8000	S A
	Lupinus obtusilobus	7–8500	8000	S A
elynae	*Carex spectabilis*	75–8500	8500	S A
gigaspora	*Lupinus albicaulis shastensis*	4–8000	7–8000	S A
	Lupinus obtusilobus	7–8500	8000	S A
herbarum	*Agrostis thurberiana*	8–8250	8250	S A
	Arnica viscosa	8–8500	8250	S A
	Eupatorium occidentale	5–7000	5500	S A
permunda	*Anemone occidentalis*	7–9000	8500	S A
	Arabis platysperma	6–9000	7000	S A
	Castilleja pinetorum	5–8500	5000	S A
	Cycladenia humilis	6–8500	7500	S A

	Ligusticum grayi	5–8500	8000	S	A
	Monardella odoratissima	4–8500	8000	S	A
	Pentstemon gracilentus	7–8500	8000	S	A
trichostoma	*Juncus balticus montanus*	5–8000	8000	S	A
Pleurotus petaloides	*Abies magnifica shastensis*	55–8500	8000	S	P
Polythrincium trifolii	*Trifolium involucratum fimbriatum*	45–5000	5000	P	A
Polyporus abietinus	*Abies magnifica shastensis*	55–8500	8000	P	P
alboluteus	*Abies magnifica shastensis*	55–8500	75–8000	S	P
elegans	*Prunus emarginata*	4–6000	5000	S	P
	Chaparral sticks		4–7000	S	P
leucospongia	*Abies magnifica shastensis*	55–8500	6–9000	S	P
	Arctostaphylos patula	4–8500	5500	S	P
	Pinus albicaulis	7–10000	8–9000	S	P
	Tsuga mertensiana	65–8500	7800	S	P
perennis	humus		55–7500	S	P
Poria lenis	*Abies magnifica shastensis*	55–8500	8000	S	P
rufa	*Pinus ponderosa*	4–7000	7000	S	P
vaporaria	*Tsuga mertensiana*	65–8500	7500	S	P
Pseudoplectania fulgens	humus		6–8000	S	P
Puccinia calochortii	*Calochortus nudus*	5–5700	5500	P	A
caricis	*Carex amplectens*	45–5700	45–5000	P	A
	Carex kelloggii	4–6000	4–6000	P	A
chamaesarachae	*Chamaesaracha nana*	45–8000	45–6000	P	A
cruciferearum	*Cardamine bellidifolia pachyphylla*	8–9500	9000	P	A
extensicola	*Carex brainerdii*	5500	5500	P	A
glumarum	*Bromus carinatus*	4–5000	4–5000	P	A
	Elymus glaucus	4–6000	4–5000	P	A
	Elymus glaucus jepsonii	5000	5000	P	A
	Sitanion hansenii	4–6000	4–6000	P	A
	Sitanion hystrix	4–9000	4–8000	P	A
harknessii	*Stephanomeria lactucina*	4–6000	4–5500	P	A
hieracii	*Agoseris scorzoneriaefolia*	80–9000	9000	P	A
	Hieracium albiflorum	4–7000	4–6000	P	A
heucherae	*Mitella pentandra*	45–8000	4500	P	A
jonesii cymopteri	*Cymopterus terebinthinus*	4–8000	5000	P	A
ligustici	*Ligusticum grayi*	5–8500	7500	P	A
mellifera	*Salvia sonomensis*	4–5000	4–4500	P	A
menthae	*Monardella odoratissima*	4–8500	5–6000	P	A
monoica	*Arabis platysperma*	6–9000	6–7000	P	A
oxyriae	*Oxyria digyna*	75–10000	9500	P	A
palmeri	*Pentstemon menziesii davidsonii*	75–9000	8500	P	A
	newberryi	5–8000	5–6000	P	A
pattersoniana	*Sitanion hansenii*	4–6000	5700	P	A
pentstemonis	*Pentstemon deustus typicus*	4–5500	4500	P	A
pimpinellae	*Osmorhiza nuda*	5–5700	5000	P	A
poae-sudeticae	*Poa pratensis*	4–8000	5000	P	A
pseudocymopteri	*Cymopterus terebinthinus*	4–8000	5000	P	A
rubigo-vera	*Holcus lanatus*	3500	3500	P	A
	Trisetum spicatum	8–8500	8250	P	A
rufescens	*Pedicularis densiflora*	4–5000	5000	P	A
scandica	*Epilobium clavatum*	8–8500	8500	P	A
subdecora	*Brickellia grandiflora*	5–5500	5250	P	A
vagans	*Godetia quadrivulnera*	4–5500	4500	P	A
vagans gayophyti	*Gayophytum ramosissimum*	4–8000	4–8000	P	A
Pucciniastrum goeppertianum	*Vaccinium caespitosum*	75–8500	75–8000	P	P
myrtillii	*Vaccinium caespitosum*	75–8500	7500	P	A
pustulatum	*Epilobium adenocaulon*	4000	4000	P	A
sparsum	*Arctostaphylos patula*	4–8000	4–5500	P	A

Pyrenophora fenestrata	*Castilleja pinetorum*	4–5000	5000	S	A
hispida	*Aster shastensis*	4–9000	6000	S	A
Ramularia delphinii	*Delphinium pauciflorum*	5700	5700	P	A
obducens	*Pedicularis densiflora*	35–5000	3500	P	A
senecionis carniolica	*Senecio aronicioides*	5–7500	5–6000	P	A
Rhizopogon brunescens	hypogaeous		8000	S	P
exiguus	hypogaeous		8000	S	P
occidentalis	hypogaeous		8000	S	P
provincialis	hypogaeous		8000	S	P
separabilis	hypogaeous		8000	S	P
Rhynchospora exasperans	*Lupinus obtusilobus*	75–8500	8000	S	A
Sarcosphaera coronaria	humus		4–8000	S	P
Scelobelonium melanosporum	*Anemone occidentalis*	7–9000	8500	S	A
	Juncus balticus montanus	5–8000	8000	S	A
	Pentstemon gracilentus	7–9000	8000	S	A
Scolecotrichum graminis	*Bromus marginatus*	4–5000	4500	W	A
	Elymus glaucus	4–6000	5000	W	A
	Glyceria elata	5–5700	5000	W	A
	Sitanion hansenii	4–6000	5700	W	A
	Stipa occidentalis	4–8500	5000	W	A
Secotium nubigenum	*Abies magnifica shastensis*	55–8500	8000	S	P
pingue	*Abies magnifica shastensis*	55–8500	8000	S	P
Sedecula pulvinata	hypogaeous		7500	S	P
Selenophoma donacis obtusa	*Elymus glaucus*	4–6000	5000	W	A
	Sitanion hansenii	4–6000	4–6000	W	A
	Sitanion hystrix	4–9000	4–9000	W	A
Sepedonium chrysospermum	*Abies magnifica shastensis*	55–8500	8000	S	A
Septoriella sp.	*Lupinus obtusilobus*	7–8500	8000	S	A
Septoria marginata	*Acer glabrum*	5–6500	5500	P	A
?petroselini	*Ligusticum grayi*	5–8500	5500	P	A
pruni	*Prunus demisa*	35–5000	4500	P	A
shastensis	*Aster shastensis*	4–9000	4500	P	A
Serpula americana	*Abies magnifica shastensis*	55–8500	75–8000	S	P
Solenia candida	*Abies magnifica shastensis*	55–8500	8000	S	P
Sphaeridium luteum	*Abies magnifica shastensis*	55–8500	8000	S	P
Sphaeropsis microscopicum	*Castilleja arachnoidea*	7–8500	8000	S	A
Stemphyllium sp.	*Monardella odoratissima*	4–8500	8000	S	A
Sphaerotheca epilobii	*Epilobium hornemanii*	5700	5700	P	A
	Epilobium lactiflorum	8000	8000	P	A
humuli	*Viola purpurea*	55–8000	6000	P	A
humuli fuliginea	*Arnica mollis*	7–8500	7500	P	A
Synchytrium asari	*Asarum hartwegii*	4–8500	5000	P	A
?aureum	*Ligusticum grayi*	5–8500	5500	P	A
Taphrina castanopsidis	*Castanopsis chrysophylla*	4–6500	4-6500	P	A
confusa	*Prunus demisa*	35–5000	5000	P	A
flectens	*Prunus emarginata*	4–6000	4–5000	P	P
potentillae	*Potentilla glandulosa nevadensis*	4–6000	5–5700	P	A
pruni-subcordatae	*Prunus subcordata*	4–4500	4500	P	P
Teichospora megastega	*Chrysothamnus bloomeri angustatus*	4–9000	8000	S	A
Tilachlidium tomentosum	*Abies magnifica shastensis*	55–8500	8000	S	A
Titaea sp.	*Arnica viscosa*	8–8500	8000	S	A
Torula crustacea	*Salix scouleriana*	4–6500	6500	S	A
Trametes pini abietis	*Abies magnifica shastensis*	55–8500	8000	S	P
Tremellodon gelatinosus	*Abies magnifica shastensis*	55–8500	8000	S	P
Trichosphaeria solaris	*Abies magnifica shastensis*	55–8500	8000	S	P
Tulasnella fuscoviolacea	*Abies magnifica shastensis*	55–8500	8000	S	P

Tulostoma tuberculatum	humus		6500	S P
Tympanis pinastri	*Abies magnifica shastensis*	55–8500	8000	S P
	Pinus albicaulis	7–10000	8000	S P
Typhula sp.	*Castilleja miniata*	5–8500	8500	S P?
	Hulsea nana	85–9500	9500	S P?
	misc. herbage		8–8500	S P?
Urocystis agropyri	*Elymus glaucus*	4–6000	5500	P A
sorosporioides	*Anemone occidentalis*	7–9000	7000	P A
Uromyces amoenus	*Anaphalis margaritacea*	5–6000	5500	P A
aureus	*Allium validum*	55–8500	55–7500	P A
fabae	*Lathyrus lanzswertii aridus*	4-6000	5000	P A
	Vicia americana	5–6000	5000	P A
hyperici	*Hypericum formosum scouleri*	4000	4000	P A
intricatus	*Eriogonum latifolium nudum*	4–5500	4–5000	P A
	Eriogonum marifolium	7–9000	75–8000	P A
	Eriogonum umbellatum polyanthum	5–7000	5500	P A
junci	*Juncus parryi*	7–8500	7500	P A
proëminens	*Euphorbia crenulata*	4500	4500	P A
spragueae	*Calyptridium umbellatum*	4–9000	7–9000	P A
Ustilago bromivora	*Bromus carinatus*	4–5000	5000	P A
	Bromus tectorum	4–6000	5000	P A
hypodytes	*Sitanion hansenii*	4–6000	57–6000	P A
	Sitanion hystrix	5–9000	7–9000	P A
	Stipa californica	4–8500	57–8000	P A
	Stipa occidentalis	4–8500	57–8000	P A
minima	*Sitanion hystrix*	5–9000	8000	P A
shastense	*Polygonum shastense*	7–9000	8000	P A

It may be noted that this table includes records of 154 genera of fungi including 274 species and 358 records of saprogenic and pathogenic activity on the part of fungi on more than half of the nearly 500 known species of vascular plants on Mount Shasta.

Notes and Discussion

Achene Characters in the Genus Scirpus

A. C. Martin

Alan A. Beetle's key to species of Scirpus based on achenes [Amer. Midl. Natur. **29**(2):533-538, 1943] proved disappointing to interested members of our staff despite the avowal that it was prepared primarily for wildlife studies.

Scirpus achenes have been encountered frequently in stomachs of wildlife and in a large proportion of instances our resulting determinations have been "Scirpus sp." Though achenes of certain species such as *robustus*, *paludosus*, *nevadensis*, *fluviatilis* and *torreyi* are distinctive enough to present no problem in identification, the difficulty and danger involved in attempting to distinguish some of the other species important to wildlife has frequently necessitated noncommital conservatism. Unfortunately Beetle's key does not alter this situation; "Scirpus sp." will need to continue in common use. In fact it is our opinion that it is impracticable to construct keys for certain of the species.

Several members of our organization have been interested in the more important species of Scirpus for nearly 15 years and have studied and collected specimens from various parts of the country. It is on the basis of this extensive experience and reference material that the key appears inaccurate and some of its basic criteria are found to be weak or definitely incorrect. Attention was focused almost exclusively on that part of the key dealing with the more important species; the remainder of the key was not studied.

It has been our experience that slight differences in color can not be relied upon to identify species. For this reason the color characters cited to distinguish such species as *acutus*, *heterochaetus*, *validus*, *americanus* and *olneyi* cannot be regarded as a safe means of identification.

As to shape characters, the key designation "wholly lenticular" appears to be wrong for both *validus* and *californicus*. Our specimens of both species vary between plano-convex and lenticular on an approximately 50-50 basis. "Trigonous" for *acutus* is not substantiated in our specimens from various parts of the country; plano-convex forms constitute the bulk and the remainder are lenticular with the exception of occasional trigonous achenes. According to our information *heterochaetus* is more likely to be trigonous than *acutus* but instead of being consistently "obscurely trigonous" a large proportion of its achenes are plano-convex. Furthermore the seed coat characters of "reticulation" and "venation" do not seem distinctive of *heterochaetus* as compared to other members of the Lacustres group. The width of *validus*, cited as 2 mm., is seriously incorrect; achenes of this species generally vary between 1.3 mm to 1.6 mm in width and are normally smaller than *acutus* rather than larger.

In addition to the major errors cited above the following minor ones were noted:

S. robustus should be 34 in the key; *rubiginosus* should be 35.

S. tuberosus (43) is omitted from the key.

The statement under "8" should be 3 mm. long or less instead of "3 mm. long."

The illustrations of *S. saximontanus* and *S. uninodis* var. *hallii* seem to be reversed; the former is the smaller of the two (see Beetle, A. A. Studies in the Genus Scirpus L. V. Notes on the Section Actaeogeton Reich. Amer. Jour. Bot. **29**(8):653-656, 1942). Also the shape of *saximontanus* (fig. 44) is illustrated incorrectly according to the same article; it should be plano-convex instead of triangular.

Fish and Wildlife Service,
Washington, D. C.

Luzula saltuensis in Illinois

G. Neville Jones

The recent discovery of this wood-rush in the northern part of Illinois represents, according to published reports, and data available in the Herbarium of the University of Illinois, an extension of the known geographical range of this species. The total known number of species of Luzula in Illinois is now four, the others being *L. bulbosa*, *L. echinata*, and *L. multiflora*. The plants were collected on a moist wooded bank in Starved Rock State Park, La Salle Co., Illinois, April 27, 1940, *C. D. Fuller* 2084, and June 16, 1943, *G. N. Jones & G. D. Fuller* 15746. The specimens (fruiting) of the later collection have been deposited in the Herbarium of the University of Illinois, and in the Gray Herbarium of Harvard University.

The nearest previous report was from Indiana, where Deam[1] cites only two collections from that state, one from Hamilton, De Kalb Co., and the other from Notre Dame, St. Joseph Co., both localities, as would have been expected, in the northern part of Indiana.

Luzula saltuensis, formerly confused with the Eurasian *L. pilosa* L., and *L. vernalis* Lam. & DC., was clearly distinguished and described by Fernald[2] in 1903, but thirty-five years later he expressed the view[3] that it is merly a variety of *L. carolinae* Wats. of the mountains of North Carolina and Tennessee. *L. saltuensis* has been attributed to Kamtchatka, but according to Hultén the Kamtchatkan plant is *L. japonica* Buch. Our species, therefore, is to be regarded as a strictly North American plant.

UNIVERSITY OF ILLINOIS,
URBANA, ILL.

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1 Deam, C. C. Flora of Indiana. 300. 1940.
2 Rhodora **5**:193-196. 1903.
3 Ibid. **40**:404. 1938.
4 Kung. Sv. Vet. Akad. Handl. **5**:225. 1928.

Book Reviews

TEXTBOOK OF CLINICAL PARASITOLOGY INCLUDING LABORATORY IDENTIFICATION AND TECHNIQUE. By David L. Belding. D. Appleton-Century Co., Inc., New York and London, 1943. xxi + 888 pp. 279 figs. and 44 tables. $8.50.

With the world becoming progressively smaller because of the development of modern means of transportation and travel, medical men as well as biologists in America are becoming increasingly aware of the importance of parasitic fauna of the tropics and subtropics and its enormous significance to the welfare of mankind. This realization has been accentuated since the entrance of the United States in the present world conflict because of the necessity of distributing men in areas where the major disease problems differ so greatly from those present in the North Temperate Zone. The health and lives of our fighting men in the tropics are being constantly endangered because of 1) the ignorance of the men themselves, and 2) the lack of information on the part of the medical officers who accompany them. The medical schools of the United States and not the medical officers, are responsible for the effects of the parasitic infections to which many of our soldiers will be subjected in the foreign lands and later in America. Because of the very nature of some of these diseases (wuchereriasis, leishmaniasis, etc.) many of our soldiers, sailors, and marines will first manifest clinical symptoms after they have been home for months and even years. Obviously our physicians have had a deplorable lack of training in tropical medicine and hygiene which bespeaks itself of another form of isolationism with concern only for diseases peculiar to our country. One of the first reactions to the awakening of American medicine to a broader education has manifested itself in the appearance of Belding's *Textbook of Clinical Parasitology*.

Though not a parasitologist, the author has assembled and organized a voluminous mass of information in a clear and concise manner. The profuse and excellent illustrations of life-history stages, comprehensive life-cycle charts, and organs and hosts showing pathogenic effects greatly facilitate the student's task of informational acquisition. The generous presence of tables summarizing heterogeneous data in regard to differential characteristics, diagnoses, distribution, transmission, taxonomy, and intermediate hosts augment the value of this volume as a textbook of human parasitology. Zoologists will appreciate the careful detail which has been taken in regard to citation of scientific names. The original author or authors and also those concerned with generic changes, if any, as well as dates are given in each case. It is the opinion of this reviewer that Dr. Belding has given zoologists a publication which commands a great deal of appreciation as well as a standard for them to aim at in the preparation of similar and/or related information.

Chief criticism may be directed toward an omission of the common and scientific names of many intermediate hosts (e.g. fishes in regard to *Diphyllobothrium latum*, and *Clonorchis sinensis*). Negligible criticism may be made concerning rather free use of generalities in the discussion of certain of the parasite groups and general considerations concerning parasitological phenomena. For instance the annelids are cited (p. 5) as possessing rare parasitic representatives when as a matter of fact many of the Hirudinea are parasitic as are all members of the family Branchiobdellidae. Reservoir hosts (p. 11) are said to be "Animals that harbor the same species of parasites as man." Obviously all hosts both intermediate and definitive would be reservoir hosts according to this statement. "Distribution of the parasite in the body of the host is determined by the method of entry, tissue-selectivity, and by the resistance of the host" (p. 15) is not wholly correct since parasites actively penetrating the skin, e.g. *Schistosoma*, *Necator* do not infect similar tissues and neither do many parasites which are ingested. A teleological trend of thought occasionally makes its presence but probably should not be judged too harshly. Particularly striking is the consistent use (pp. 5, 10, 14, etc.) of a word spelled "parthogenesis" which the author apparently intended for *parthenogenesis*.

The shortcomings of the text are greatly outweighed by the merits of the volume and the work is recommended highly as a text for medical schools and to individuals interested in human parasitology. It is sincerely hoped that a future edition will contain corrections and additions which will place this work with the best volumes in this field of endeavor. —J. D. MIZELLE.

MEDICAL PARASITOLOGY. By J. T. Culbertson. Columbia University Press, Morningside Heights, N. Y., 1942. xii + 285 pp., 21 plates, 16 figures, 7 tables. $4.25.

Although this treatise contains much good information and deals with all the groups of parasites infecting or infesting man, it is telescopic in nature and remarkably lacking in a great many seemingly necessary details. Diagnostic methods are so inadequate that it is impossible, for instance, to identify the trophozoite of *Entamoeba histolytica* and the description of this stage of the parasite (p. 75) is too incomplete to be of use in this regard. Only one species of *Glossina* is given as an intermediate host for each of *Trypanosoma gambiense* (p. 97) and *T. rhodesiense* (p. 103). Intestinal species of the Endamoebidae, except *E. histolytica*, are given so little attention that the reader has no way of knowing that they inhabit the large intestine (p. 83). A "reservoir" (p. 11) is so generally defined that it includes both intermediate and definitive hosts. "Species which observe a parasitic existence are found in all phyla of the animal kingdom" (p. 15) is not true and neither is the statement (p. 28) that *Trypanosoma gambiense* is transmitted by sexual intercourse. The plates and figures are both poor and excellent. Especially poor is the plate (opposite p. 127) concerning malaria and the fiure (p. 201) regarding the mouth parts of hookworms. The seven tables which summarize diagnostic procedures, geographical distribution, thereapeusis, etc. are excellent and no doubt will be appreciated by various readers. References, except for a list of books, are conspicuously absent. This and many other shortcomings readily demonstrate that *Medical Parasitology* is not a scholarly book. It is unfortunate that the author did not utilize more time and care in the preparation and presentation of his material.—JOHN D. MIZELLE.

THE GENETICS OF THE MOUSE. By Hans Grüneberg. Cambridge University Press, 1943. xii + 412 pp., 14 pls., 43 figs., 118 tables. $7.00.

A large number of the specialized disciplines of zoology have drawn upon the laboratory mouse as a source of experimental material. Hence, although this book is directed primarily to the attention of geneticists, this does not mean that anatomists, histologists, pathologists, physiologists, and other specialists cannot find in it information of use to them in their particular sphere of investigation. The wide range of subject matter in a book confined to a single animal is due in part to predominate emphasis on the problem of what the gene does, a study that of necessity touches upon many branches of biology.

The section on taxonomy following the introduction is exceedingly brief and admittedly inadequate since Dr. Grüneberg does not feel compelled to untangle the whole taxonomic snarl merely in order to pull out the two species used by geneticists, *Mus musculus* L. and *Mus bactriamus* Blyth. An ensuing section on reproduction and growth is also somewhat condensed in form since the subject has been well reviewed in a previous book by the staff of the Roscoe B. Jackson Memorial Laboratory.

It is in the following sections that the bibliography becomes comprehensive and the arrangement of subjects indicates a monographic approach. Headings are placed after the manner of a taxonomic key into progressively exclusive subdivisions. For example in Chapter IV which forms the bulk of Dr. Grüneberg's six chapters inherited differences are subdivided into the morphological and the physiological. Morphological differences are further divided into qualitative and quantitative. The author is well aware of the arbitrary nature of subdivisions at this level of abstraction and adopts the method for its expediency. Under qualitative differences there is an excellent discussion of the literature on The Integument; Endocrine Organs; Brain and Sense Organs; Blood and Blood-forming Organs; Skeleton: Alimentary Tract; Urogenital System,

with a few concluding remarks on the significance of qualitative differences and phenocopies.

Serological characteristics of mice as well as numerous other attributes of a physiological nature, are discussed. The genetic basis of resistance to infectious diseases is considered at some length and provides detailed criteria by which the too often uncritical work in this field can be evaluated.

Chromosomal inheritance and induced genetic changes are the subject of Chapters V and VI. Two appendices follow. The first by C. C. Little and P. A. Gorer, deals with the genetics of cancer in mice and reviews in a relatively few pages the truly remarkable knowledge that has been obtained concerning spontaneous and induced tumors. A second appendix gives methods for the keeping and breeding of mice.

Dr. Grüneberg has written an excellent book. His training in medicine and biometry and his numerous original contributions to the literature undoubtedly aid him in achieving a well balanced approach to a diversified subject. It is the reviewer's opinion that "The Genetics of the Mouse" should be owned by geneticists and should at least be available as a reference to biologists everywhere.—VERNON BRYSON, Biological Laboratory, Cold Spring Harbor, L. I.

HANDBOOK OF SALAMANDERS: THE SALAMANDERS OF THE UNITED STATES, OF CANADA, AND OF LOWER CALIFORNIA. By Sherman C. Bishop. Comstock Publishing Co., Ithaca, N. Y. 1943. xiv + 555 pp., colored frontispiece 144 figs., 55 maps, 1 pl. $5.00.

The appearance of an adequate account of the salamanders of North America north of Mexico is a most gratifying herpetological event. By means of Dr. Bishop's book, every species and subspecies in the United States can be accurately named. Each of the 126 named forms is figured and its geographic range is shown on an accompanying map. Additions to our knowledge of the ranges and of the ecological distribution within these areas are to be expected, and offer interesting minor problems to the local naturalist. The colored frontispiece illustrates the Texas newt.

Dr. Bishop is well known for his work on the life histories of the salamanders of New York, and this interest is shown in the excellent summaries of the breeding habits of each species. It is this branch of the natural history of these creatures that offers a stimulating field for further search. There are large unknown segments in the life histories of many of the forms, and even though the habit is well-known, the discovery of a dusky salamander brooding her eggs in her earthen nest, or of the tiny red-backed salamander with its grape-like cluster of eggs suspended from the roof of a cavity in a rotten log is still a never-to-be-forgotten experience.—KARL P. SCHMIDT.

DISEASES AND PESTS OF ORNAMENTAL PLANTS. By Bernard O. Dodge and Harold W. Rickett. The Jaques Cattell Press, Lancaster, 1943. xi + 638 pp., 192 figs. $6.50.

This book fulfills a need frequently experienced by people endeavoring to cultivate ornamental plants in gardens and in greenhouses. For the first time the diseases of these plants and their control measures are dealt with in a single volume. Although prepared primarily for gardeners rather than professional botanists, this approach has not greatly detracted from the scientific character of the material presented.

Written by two staff members of the New York Botanical Garden, the treatment of the material is authoritative but limited to the diseases of the more important ornamental plants of the United States and the more common and readily applicable means of control. For example, in the case of mealy bugs, the insect parasites employed for the conrtol of these pests are not mentioned, although they can be used with success. Perhaps the authors are justified in excluding such material, because this method is not likely to succeed in the hands of the average gardener.

The book opens with an introduction (118 pages) to the study of various types of diseases of plants, intended to provide an adequate background for the amateur gardener. The fundamentals of plant pathology are presented here in simple non-technical language

and illustrated wiith an abundance of clear and well chosen figures. Unfortunately, the degree of magnification is not given and as a result illustrations of objects magnified several hundred times mean little to the person not already familiar with them.

The second part of the book contains an alphabetical list of some six hundred species of garden and greenhouse plants arranged according to genera; under each species are given its important diseases and the methods of their control. A list of twenty-three more or less general references on diseases of certain groups of ornamental plants is appended. A general index containing the common names of plants, of diseases, and of disease producing organisms concludes this serviceable book.—N. L. NOECKER.

THE EMBRYOLOGY OF LARIX. By James Morton Schopf. University of Illinois Press, Urbana, 1943. Illinois Biological Monographs **19**(4):97 pp., 47 figs., 7 pls. $1.50.

Many of our present ideas of tissue- and organ-differentiation in conifer-embryos have necessarily been based upon the situation in *Pinus*. For this reason, morphologists should welcome this important contribution by Dr. Schopf devoted to a detailed analysis of the complete embryology of *Larix decidua* Mill. The author makes clear in the preface his conviction of the importance of a dynamic approach to embryological inquiry. He succeeds admirably in applying this attitude in both his description and his interpretation of the histogenetic data. Far too often, in the reviewer's opinion, embryological details are highly formalized and the successive steps in ontogeny presented in such a static manner as to eliminate even the obvious "dynamics" of the entire phenomenon. This type of formalism is conspicuously absent in Dr. Schopf's treatment and is well illustrated, for example, by the inclusion of a chart summarizing chronologically the embryologic sequence of histogenetic processes.

It is neither feasible nor appropriate to attempt a discussion of the extremely detailed exposition of embryology presented in Dr. Schopf's treatise. The facts are clearly set forth and the important features of each step in ontogeny are illustrated by good line-drawings and very helpful photomicrographs. The reviewer personally objects to the terms, "pro-stage," "meta-stage," "ana-stage" and "telo-stage," which are applied to the four major phases of embryology. Furthermore, the constant use of the original terminology of Hanstein (i.e. dermatogen, periblem and plerome) seems quite unjustified in view of the lack of sharp "determination" of tissue-boundaries in the embryo of *Larix*. But these are probably minor objections and should not detract from the general value of the data. One point of detail in the author's discussion of the mature embryo of Larix, however, seems very inadequately treated, viz., the significance of the absence of a "dermatogen" in the plumular-apex. It would have been desirable, in the reviewer's opinion, to examine this fact in the light of recent studies by several investigators on the cellular structure of the shoot apex of mature gymnosperm sporophytes. These studies demonstrate clearly that in many conifers, as well as in *Ginkgo* and the cycads, a distinct tunic layer or "dermatogen" *never* becomes established in the apex. This fact is morphologically and possibly phylogenetically significant when it is realized that a surface tunic usually arises *early* in the embryology of angiosperms and typically *persists* throughout the post-embryonal phases of growth of the shoot apex.

Dr. Schopf concludes his monograph by a thoughtful and suggestive examination of the embryology of gymnosperms in the light of Bower's concept of the "primitive spindle." While essential agreement exists between certain aspects of embryology in many vascular cryptogams and the gymnosperms, two important distinctions are recognized, viz.: (1) delayed establishment of "polarity units" (i.e. apical cell units) in the gymnosperms and (2) the origin of the primary root in gymnosperms as an axial structure intercalated between the suspensor and the plumular apex. Since the primary root of vascular cryptogams with a suspensor is lateral in origin, this is regarded as a fundamental distinction. Indeed, the author maintains that "it is one of the strongest arguments for a monophyletic derivation of the gymnosperm phylum as a whole, and it may possibly apply to a larger group of seed plants."—ADRIANCE S. FOSTER, University of California.

TEXTBOOK OF BOTANY. By E. N. Transeau, H. C. Sampson, and L. H. Tiffany. Harper & Brothers Publishers, New York, 1940. xi + 812 pp., 4 colored pls., 424 figs. $4.00.

WORK BOOK IN GENERAL BOTANY. A Problem Approach to Plant Science through Observation and Discussion. By H. C. Sampson. Harper & Brothers Publishers, New York, 1941. 242 pp., illus. $1.75.

The teaching of general botany has in recent years been the subject of many discussions and experiments. The Department of Botany of Ohio State University has been one of the moving forces aimed at rejuvenation of the teaching of general botany. The *Work Book*, an integral part in this program, has grown to its present size with the experience gained by the author while using the new method over a period of years. Incorporated are ample instructions, questions, reviews and drawings to accommodate a wide range of subject matter for suitable laboratory and field work. Thus it is unquestionably the largest and most thorough laboratory manual of its kind available. Students who have mastered its contents are bound to have acquired a sound foundation in botany.

By comparison, the *Textbook of Botany* reflects the experience gained by its authors in teaching general botany according to the new plan. Like the *Work Book* the *Textbook* also departs widely from customary practices of presenting general botany. For instance, of the 53 chapters only eight chapters are allotted either wholly or in part to a survey of the plant kingdom. Most of the chapters are, therefore, concerned with the important physiological and structural aspects of the higher and lower plants, their usefulness or pathology, ecological subjects, heredity and evolution. In short, no significant field of botanical knowledge has been omitted and many are here treated more extensively than elsewhere. The illustrations are largely original, on the whole well chosen and excellently prepared for the greatest possible benefit of the student. The addition of several colored plates in a general textbook is a remarkable advancement in the direction of humanizing botany.

No doubt a great deal of interesting material, e.g., the chapter on the "Origin of Plants Used by Man," could be included by limiting the survey of the plant kingdom. Such changes are certainly based on the fact that the average student is more interested in general information of this sort than in detailed life histories of many lower and higher forms. By the same token, however, the student may find it equally difficult to follow some of the chemical details included in the first part of the book, since he is not likely to have had sufficient training in chemistry by that time. Irrespective of this difficulty, the *Textbook of Botany* represents a notable achievement in teaching general botany, because the emphasis is definitely placed on living plants and plant communities. Such an approach, supported by the present realization of the immense importance of plant foods and products in human economy, should bring more students to a better appreciation of plant life than they were prone to admit only a few years ago.—THEO. JUST.

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